FIRE AND SUCCESSIONAL TRAJECTORIES IN BOREAL FOREST: IMPLICATIONS FOR RESPONSE TO A CHANGING CLIMATE

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By

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Fairbanks, Alaska

August 2003

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ABSTRACT

Because of the key role played by fire in structuring boreal forest ecosystems, interactions between vegetation and fire regime may be an important and dynamic control of forest response to climate change. This research uses a series of field observations and experiments in boreal forests to examine the nature of several potential fire and vegetation interactions, and how such interactions may influence forest response to climate change. Long-term observations of post-fire succession provide information on the timing of tree establishment and the effects of early establishment on subsequent successional trajectories. The role of competitive interactions in driving patterns of early establishment was tested with experimental manipulations of aspen (*Populus tremuloides*) cover after fire. This research demonstrated that competition by aspen re-sprouts may reduce the success of conifer establishment and favor long-term dominance by deciduous trees. The effects of fire severity on successional trajectories were tested in a series of field experiments that contrasted patterns of seedling establishment across differences in depth of the post-fire organic layer. All species in the experiment responded negatively to decreased fire severity, but deciduous trees were more sensitive in their response than conifers. Thus, variations in burn severity are likely to mediate deciduous establishment in organic-rich stands. Observations of natural tree regeneration in stands that burned at different ages also indicate that a decrease in fire interval can influence the relative abundance of deciduous and coniferous species by reducing conifer establishment. Over longer time scales, changes in biota caused by species migration may

influence fire and vegetation interactions. Observations of post-fire regeneration at the current distribution limits of lodgepole pine (*Pinus contorta*) indicate that continued range expansion of pine could initiate rapid shifts in dominance from spruce to pine within a single fire cycle. Together, these results provide insight into the dynamic feedbacks between fire and vegetation that can lead to high levels of system resilience, while also promoting rapid responses when threshold conditions are crossed. A more complete understanding of these interactions will improve our ability to manage and predict boreal ecosystem responses to a changing climate.

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ACKNOWLEDGEMENTS

I gratefully acknowledge financial support for this research from the following sources: Bonanza Creek LTER support from NSF (grant DEB-0080609) and USDA Forest Service (grant PNW01-JV11261952-231), a student research grant from the Center for Global Change and Arctic System Research at the University of Alaska, a Northern Research Endowment Grant from the Northern Research Institute at Yukon College, and graduate fellowship support from NSERC Canada (PGSB-222640-1999) and NASA Headquarters under the Earth System Science program (ESS/00-0000-0191). Additional, in-kind support was provided by the Forestry Branch of the Department of Indian and Northern Affairs Canada and the University of Alaska Fairbanks. The Alaska Division of Forestry provided black and white spruce seed for the experimental studies. Permission to use lands for experimental work was provided by the U.S. Army base at Fort Greely (Delta, Alaska), the Bonanza Creek LTER (CPCRW, Alaska), the Yukon Heritage Branch (Campbell Highway, Yukon) and the Ta'an Kwatchan First Nation (Fox Lake, Yukon).

The research described here would not have been possible without the contributions of many people. I am particularly grateful to F. S. (Terry) Chapin, III for both supporting and challenging me in his capacity as a thesis advisor, and to Jonathan Henkelman for technical expertise and spousal support throughout the project. I would also like to acknowledge the input provided by members of my graduate committee at UAF, Dave McGuire, Roger Reuss, and Marilyn Walker. Completion of the field work

for this research relied heavily on the involvement of several undergraduate research assistants: Eliza Bettinger and Kim Jansen (2000), Ben Legler and Heather Smith (2001), and Erica Close and Sasha Oystryk (2002). I also gratefully acknowledge the assistance in the field and laboratory of many volunteers, co-workers, and collaborators, namely, Britt Arnesen,Wim Arp, Belle Bergner, Monika Calef, Monique Heijmans, Jefferson Jacobs, Eric Kasischke, Heidi Kristensen, Rob LeGare, Tracey Martinson, Heather McIntyre, Amber Moody, Scott Rupp, Catharine Thompson, Dan Uliassi, and members of the 2002 Ecosystems of Alaska class at UAF.

The long-term observations described in this thesis (Chapters 1 and 5) were conducted in collaboration with F. S. Chapin, III, Joan Foote, and Leslie Viereck in the Boreal Ecosystems Co-operative Research Unit at UAF, and Sue Kemmett and Kirk Price at the Yukon Forestry Branch of the Department of Indian and Northern Affairs Canada. My role in this reasearch was to collect the most recent set of observations in the permanent plots, and to conduct the subsequent analysis and synthesis of results. My collaborators on these projects assisted with field work and provided comments on drafts of the resulting manuscripts. The long-term studies that provided the basis of this research were initiated by the Institute of Northern Forestry at UAF and Forestry Canada. In all other chapters of this thesis, I took the lead role in the design, implementation, and synthesis phases of the research. F. S. Chapin, III contributed in an advisory capacity to many of these projects, and is included as a co-author for those publications.

CHAPTER 1: INTRODUCTION

Interactions between climate, fire, and vegetation in the boreal forest

General circulation models (GCM's) project significant increases in mean annual temperature over the next century, particularly at high latitudes, as a result of human-induced increases in radiatively active trace gases such as CO2 (Kattenberg *et al.*, 1996). Several models relating boreal forest vegetation to GCM climate projections have suggested that substantial shifts in vegetation types and species dominance may occur in response to direct effects of climate on plant growth and survival (*e.g.* Pastor and Post, 1988; Bonan *et al.*, 1990; Prentice *et al.*, 1992; Lenihan and Neilson, 1995; Sykes and Prentice, 1995). However, fire disturbance is a dominant factor structuring boreal forest (Payette, 1992), and fire effects may strongly mediate forest responses to climate change (Suffling, 1995). Changes in fire frequency have occurred in association with climate shifts in the paleorecord (Clark, 1988; Flannigan *et al.*, 2001) and are predicted to occur in the future as a result of global climate change (Stocks *et al.*, 1998; Flannigan *et al.*, 2001).

The site-specific response of vegetation to fire depends on factors that affect the availability and establishment of propagules (Zasada *et al.*, 1992), plant competition (Cater and Chapin, 2000), plant/animal interactions (Pastor *et al.*, 1993), and feedbacks between vegetation and physical environment that affect soil temperatures, decomposition rates and nutrient availability (Bonan and Shugart, 1989; Van Cleve *et al.*, 1991). Combined with direct effects of climate on plant growth and environment, these processes shape vegetation response to climatic change. Over longer scales of time and space, changes in climate and disturbance regime interact with patterns of species

migration to determine landscape vegetation dynamics. Climate change appears to be an important driver of species migration patterns, which in turn affect the pool of species that are available to interact at a given location (Webb, 1987; Huntley, 1992). The dynamics of biotic and abiotic interactions are further modified, however, by the spatial scale, type, frequency, and severity of disturbances acting on a landscape. Together, these properties of disturbance regime govern the relative proportion of the ecosystems in different stages of succession and affect the distribution of propagules available for post-disturbance recovery (Turner *et al.*, 1997; Thompson *et al.*, 1998). Changes in vegetation may themselves influence disturbance regime and climate (Chapin *et al.*, 2000), generating the potential for complex interactions to occur between these three factors. In particular, positive feedbacks between traits of individual species and their environment can, once initiated, lead to establishment and maintenance of community types that represent alternative, self-maintaining ecosystem states (Frelich and Reich, 1999; Petraitis and Latham, 1999).

In the boreal forest, stand types differ in traits relating to post-fire recovery and stand flammability. Differences in growth rates and understory composition may affect the amount of time required for a stand to accumulate fuels and reach a burnable state (Li *et al.*, 1997; Schimmel and Granström, 1997). Boreal tree species also differ in moisture content and flammability, with deciduous species generally having lower flammability than coniferous species (Hély *et al.*, 2001). These traits are likely to affect minimum fire return interval and fire severity (Wang, 2002). Fire characteristics, in turn, affect the colonization potential of boreal tree species with different post-fire recovery strategies

(Zasada *et al.*, 1992; Greene *et al.*, 1999). Interactions between species traits and fire regime can reinforce species dominance through multiple fire cycles, if the fuel characteristics of a stand tend to result in a fire regime that favors the re-establishment of the stand dominant (Frelich and Reich, 1999; Mann and Plug, 1999). Where environmental conditions are suitable for the establishment of different species associations, interactions between fire regime and vegetation composition may generate several possible successional trajectories for a given site. Furthermore, if the development of alternative succession trajectories is sensitive to changes in climate, then ecosystems with multiple succession pathways may undergo rapid compositional changes in response to climate change.

Understanding the role and importance of alternative community states in ecosystem response to climate change becomes more difficult when other aspects of global change are included. Studies of invasive species have demonstrated that the appearance of species with important new functional traits can dramatically affect the structure and function of ecosystems, especially when a species has unique feedback effects on environment or disturbance regime (Vitousek *et al.*, 1987; D'Antonio, 2000; Hu *et al.*, 2001). In much of North America, boreal forest communities include rapid-growing, fire-adapted pines that occupy a niche intermediate between fast-growing deciduous species and slow-growing spruces. Boreal forests in interior Alaska, however, lack a pine component and may be open to invasion by species such as lodgepole pine (*Pinus contorta* ssp. *latifolia*), which is found in the forests of adjacent Yukon Territory. Pine forests in western Canada burn more frequently than spruce forests (Larsen, 1997),

and fires that burn through pine-dominated areas tend to be larger than fires burning in other forest types (Cumming, 2001). These patterns suggest that pine forests may influence fire regime by altering the structure or availability of forest fuels. In addition, lodgepole pine has serotinous cones that store and release seed after being heated by fire, allowing this species to rapidly re-establish following a fire (Lotan and Perry, 1983). Together, the positive interactions between fire occurrence and pine abundance could initiate a feedback loop that would help maintain pine stands in a landscape once they have established. Indeed, lodgepole pine frequently forms self-maintaining stands that are characterized by a short fire return interval and low ecosystem carbon storage (Lotan and Perry, 1983). Lodgepole pine grows well in Alaska in plantations (Alden, 1988), and has been expanding its range westward at least as recently as 450 years ago (MacDonald and Cwynar, 1986). Continued western migration of lodgepole pine under a warmer climate or as a forestry management option could have important (but unanticipated) feedback effects on the fire regime and ecosystem functioning in Alaskan boreal forests.

Our understanding of how forest ecosystems respond to direct and indirect effects of variations in climate, disturbance, and species invasions is still very limited. In the boreal forest, interactions between climate, fire regime, and vegetation composition have the potential to generate complex ecosystem responses to climate change. This research seeks to address some of these issues through a combination of observational and experimental studies of fire and vegetation interactions in boreal forest (Figure 1.1). Several of these studies make the assumption that most stand establishment occurs within the first years after fire, in order to extrapolate early post-fire responses to later stages of

stand development. Chapter 2 presents a test of this assumption, previously based on data from stand reconstruction studies (Johnson and Fryer, 1989; Lavoie and Sirois, 1998; Gutsell and Johnson, 2002), using long-term observations of tree establishment in Alaska and Yukon Territory. Two subsequent chapters describe results from experiments in recently-burned forests that were designed to assess the importance of biotic and fire effects in driving patterns of post-fire tree establishment. The effects of aspen sucker competition on tree seedling establishment and growth after fire are tested using experimental removal of aspen in a regenerating aspen stand (Chapter 3). Results from this study have implications for the ways in which deciduous-dominated stands may perpetuate themselves over time by resisting invasion by conifers. The second experiment (Chapter 4) evaluates the role of fire severity in driving patterns of forest stand structure and composition across a range of post-fire stands. A synthetic meta-analysis is used to test the overall effects of burn severity on tree seedling establishment across multiple experiments, and to develop a conceptual model of severity effects on regeneration for different species and forest types. The effects of variations in fire frequency and severity on successional trajectories in naturally-regenerating forest stands are evaluated using a long-term dataset that documents strong responses of regeneration to variation in fire regime (Chapter 5). These data present empirical evidence of the potential for changes in fire regime, initiated by climate change or some other factor, to stimulate rapid shifts in boreal forest composition. Long-term interactions between fire, climate, and vegetation are explored in Chapter 6, through an observational study of post-fire stand regeneration at the northern distribution limits of the lodgepole pine. This study presents evidence for

continued migration of lodgepole pine, and suggests that interactions between climate and fire regime may play an important role in shaping the past and future distribution of this species.

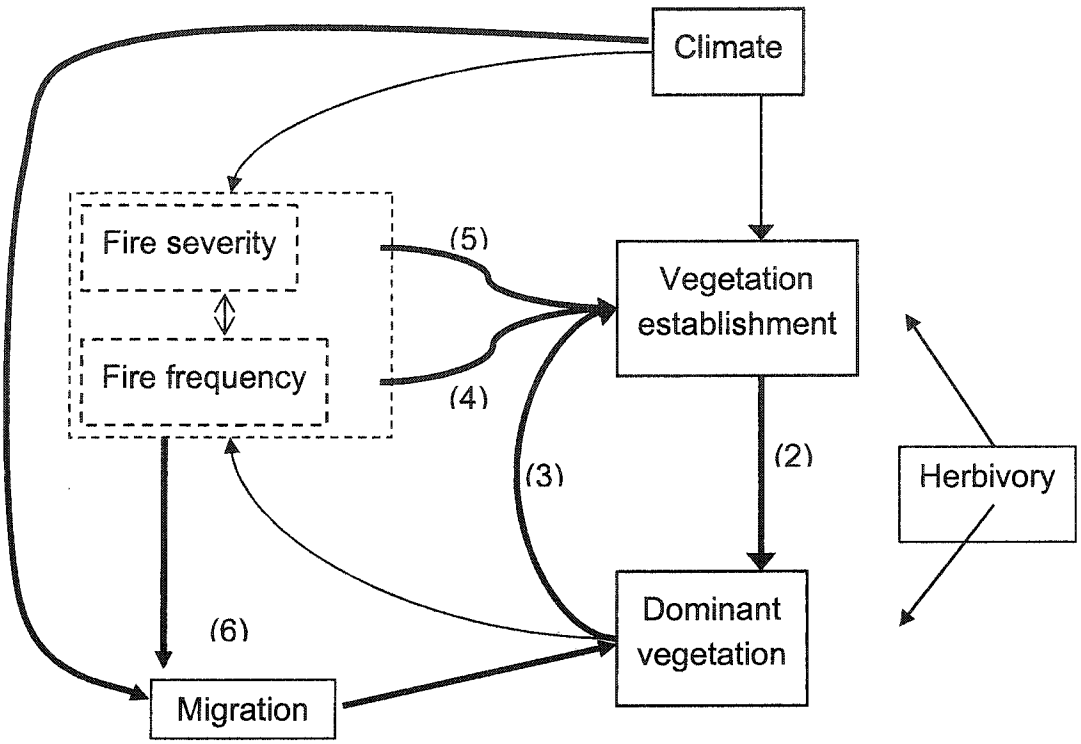

Figure 1.1: A conceptual diagram of vegetation, fire, and climate interactions in the boreal forest. Bold lines indicate pathways investigated in this thesis research, along with key chapter numbers in parentheses. Changes in climate affect patterns of vegetation establishment, fire regime, and species migration. Fire regime influences vegetation establishment and long-term migration, and is reciprocally influenced by vegetation patterns. Establishment patterns affect the composition of dominant vegetation, which in turn influence re-establishment following disturbance. In addition, other biotic agents, such as herbivory, may alter the relationship between establishment and mature vegetation.

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CHAPTER 2: TREE REGENERATION AFTER FIRE*

* Manuscript title: Long-term observations of tree regeneration following fire in boreal forests. Authors: J. F. Johnstone, F. S. Chapin, III, J. Foote, S. Kemmett, K. Price, and L. Viereck. Submitted to Canadian Journal of Forest Research.

Abstract

This paper presents data on early post-fire regeneration obtained from repeated observations of recently burned forest stands along the Yukon/British Columbia border and in interior Alaska. Measurements of tree density were made over 20-30 years following fire, providing high-resolution data to characterize patterns of early forest establishment. Recruitment rates of the dominant tree species in both study areas were highest during the first five years after fire, and additional net establishment was not observed after 10 years. Post-fire spruce (*Picea mariana* (Mill.) B.S.P. and *Picea glauca* (Moench) Voss s.l.) maintained a constant population size after the first decade in the two study areas. Populations of aspen (*Populus tremuloides* Michx.) and lodgepole pine (*Pinus contorta* Dougl. ex. Loud. ssp. *latifolia* (Engelm.) Critchfield) both declined after 10 years in mixed-species stands along the Yukon border. Rates of mortality of aspen and pine were positively correlated with the initial densities of that species, indicating that thinning occurred as a density-dependent process. At all sites, there were high correlations between measurements of stand density and composition made early vs. late in the monitoring period, indicating that patterns of stand structure initiated within a few years after fire are maintained through subsequent decades of stand development.

Introduction

Fire disturbance is a major factor driving patterns of vegetation structure and composition in boreal forest landscapes. Much of the boreal forest in North America is subject to relatively short fire return intervals of 50-150 years, and most forests in this region can be viewed as undergoing some stage of recovery from fire disturbance (Payette, 1992). Because of the high frequency of disturbance, understanding variations in vegetation composition across boreal landscapes requires knowledge of patterns of post-fire succession. To date, much of our information on successional changes in boreal forest vegetation comes from chronosequence studies, in which communities of different ages are compared to each other (*e.g.* Carleton and Maycock, 1978; Yarie, 1983; Cogbill, 1985; Foster, 1985; Zoladeski and Maycock, 1990), or stand reconstructions, where growth and establishment patterns in the past are inferred from the current stand age structure (Johnson and Fryer, 1989; Sirois and Payette, 1989; Johnson *et al.*, 1994; Galipeau *et al.*, 1997; Gutsell and Johnson, 2002). While these methods have been very productive in describing successional patterns, their utility relies heavily on assumptions that are difficult to validate and which may, in reality, often be violated. The interpretation of chronosequence studies, for example, generally requires a proviso that variations in initial conditions have had little effect on the observed patterns, an assumption that is unlikely to be true for succession in boreal forests where establishment is highly sensitive to initial conditions of seed availability or substrate quality (Zasada *et al.*, 1992) or where variations in species composition may influence other ecosystem processes (Fastie, 1995). Likewise, stand reconstructions depend heavily on assumptions

that individual trees can be correctly aged, and that age-dependent variations in survivorship are adequately detected and accounted for in the analysis. Recently, several studies have demonstrated that there can be large biases in the aging of boreal trees using standard coring procedures (DesRochers and Gagnon, 1997; Parent *et al.*, 2000; Wong and Lertzman, 2001; Gutsell and Johnson, 2002) and that improved accounting of mortality may alter the interpretation of age structures (Johnson and Fryer, 1989; Johnson *et al.*, 1994). Thus, the information on successional patterns obtained from indirect approaches such as chronosequence or reconstruction studies may incorporate several sources of error or uncertainty. Alternative sources of data that can be used to test the results from different methodologies are therefore highly valuable in interpreting the general body of research on post-fire succession. This study presents data gathered from long-term observations of *in situ* post-fire succession measured in boreal forest stands for two to three decades after fire. We use these data to test predictions of the timing of tree recruitment derived from stand reconstructions, and to evaluate the importance of early establishment patterns to subsequent stand development.

Stand reconstructions in the boreal forest frequently show that the majority of trees that compose a mature stand recruited during a short, 3-7 year period after fire (Johnson and Fryer, 1989; Johnson *et al.*, 1994; Lavoie and Sirois, 1998; Gutsell and Johnson, 2002). However, there are other studies that suggest establishment occurs over a longer period of two decades or more after fire (Carleton, 1982; Foster, 1985; Sirois and Payette, 1989; Zoladeski and Maycock, 1990; DesRochers and Gagnon, 1997). Given the uncertainty in stand age reconstructions (Wong and Lertzman, 2001), it is unclear to what

extent the reported differences in establishment patterns are due to the effects of site or vegetation factors *versus* variations in stand reconstruction methods. In this paper, we use an alternative method of direct counts of trees over time to estimate the duration of the net establishment window following fire. Direct counts also allow us to test for the onset of thinning during the observation period, another important population process that is difficult to estimate from stand reconstructions (Johnson and Fryer, 1989; Johnson *et al.*, 1994).

Patterns of early establishment in boreal forests are important to long-term successional trajectories because most of the individuals with the potential to dominate the canopy establish simultaneously after stand-replacing disturbance (Johnson and Fryer, 1989; Sirois and Payette, 1989; Johnson *et al.*, 1994; Gutsell and Johnson, 2002). Subsequent changes in forest canopy composition appear to be driven primarily by species differences in growth or mortality rates (Gutsell and Johnson, 2002). These changes can be viewed simply as modifications of the composition or density structure of a stand that was established during a short period after disturbance. A strong linkage between early post-fire establishment and subsequent stand composition has been used to justify the estimation of stand successional trajectories from data on early establishment (Lavoie and Sirois, 1998; Chapter 6). We test the hypothesis that variations in establishment drive patterns of subsequent stand composition by evaluating correlations between stand data collected within a few years after fire and data collected in the same stands two or three decades after fire.

Methods

This study uses data from two long-term monitoring programs, one along the Yukon/British Columbia border near the southeast Yukon (here referred to as the SE Yukon), and another in interior Alaska near Fairbanks, Alaska. Both studies were initiated to monitor long-term changes in vegetation following fire, and currently encompass 20-30 years of repeated observations in permanent plots. The details of the methodology and site conditions vary between the two studies and are described separately below.

Southeast Yukon study area

Long-term monitoring plots were established in 1983 following 3 large fires that occurred near Watson Lake, Yukon in 1982 (Oswald and Brown, 1990). The forest types included in the study were dominated by black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss s.l.), lodgepole pine (*Pinus contorta* Dougl. ex. Loud. ssp. *latifolia* (Engelm.) Critchfield), and trembling aspen (*Populus tremuloides* Michx.). Paper birch (*Betula papyrifera* Marsh.), balsam poplar (*Populus balsamifera* L. ssp. *balsamifera*) and western larch (*Larix laricina* (Du Roi) K. Koch) also were occasionally present in the pre-fire forest. Soils in the study area primarily consisted of Regosols and Brunisols, with occasional Gleysol types in wetter areas (Agriculture Canada, 1987; Oswald and Brown, 1990). One fire was located northeast of Watson Lake near Tom Creek (60° 13'N, 128° 55'W), and burned 8000 ha in early July, 1982. A second fire occurred near the current village of Fireside, B.C. (59° 40'N, 127° 9'W). This large fire was initiated by 3 separate lightning strikes and covered 182,000 ha between

mid-June and mid-August, 1982. The third fire in the study was human-caused and occurred near Lower Post, British Columbia (59° 58'W, 128° 30'W). It burned in late July, 1982 to a size of 1200 ha.

In 1983, 39 long-term measurement sites were established by the Canadian Forest Service, with 11, 22 and 6 sites in the Tom Creek, Fireside, and Lower Post burns, respectively. Since the study was initiated, one site has been lost from the Lower Post burn and two from the Fireside burn. At each site, measurements were made within a single, 10x10 m plot, which was divided into 5x5 m sub-plots for ease of measurement. The plots were marked by 1-m aluminum rods pounded into the ground. Sites were selectively located to include a variety of soil types, topography, and pre-fire vegetation characteristics within each burn. The plots were established along road corridors, and were originally located a least 50 m from a road right-of-way. These distances have changed for some of the plots due to subsequent changes in the routing of the Alaska Highway.

Vegetation was measured in the SE Yukon plots in 1983, 1984, 1985, 1987, 1992 and 2000-2001 (1, 2, 3, 5, 10 and 19 years post-fire). The first five years of measurements were made by researchers at Forestry Canada and are detailed in an earlier report (Oswald and Brown, 1990). Vegetation observations in each year consisted of counting and measuring the heights of all tree seedlings within a plot, and visually estimating percent cover of vegetation. Observations were made separately in each 5x5 m subsection of the main plot, and then summed or averaged to obtain an estimate for the whole plot. Seedlings of black and white spruce were pooled into a generic spruce

category because of the difficulty in consistently distinguishing between young black and white spruce. Seedling counts were based on the number of individual stems coming out of the soil, and stems that branched above the soil surface were counted as a single individual. Tree height for each stem was measured as the distance from the ground to the apical bud, using a meter stick or telescoping tree height pole. Visual estimates of vegetation cover were made for groupings of vegetation growth forms (*i.e.* trees, shrubs, herbs) and used an 8-class, semi-logarithmic cover scale (Mueller-Dombois and Ellenberg, 1974).

Interior Alaska study area

The Alaskan monitoring plots described here were located along the ridge and in the valley of Wickersham Dome, a small mountain adjacent to the Eliot Highway and approximately 50 km north of Fairbanks, Alaska. The vegetation in the area was strongly dominated by black spruce, with occasional aspen or birch trees. Most of the area was underlain by permafrost, and the mineral soil was covered with a thick moss mat in mature stands (Viereck and Dyrness, 1979). Two sets of sites are included in the study, one set that was burned by a natural wildfire in 1971, and a second set that was burned by a series of experimental burns in 1978.

The 1971 wildfire burned the hillslopes and valley of Washington Creek, adjacent to Wickersham Dome (65° 10' N, 147° 54' W, elevation 325-400 m). Five sites were established to monitor vegetation recovery following fire, two in a lightly-burned area that had live trees that survived the fire, and three in more severely-burned areas where

all the trees were killed (Viereck and Dyrness, 1979). The pre-fire stands were composed almost entirely of black spruce. The experimental burns in 1978 were located along the southwest slopes of Wickersham Dome near the ridgetop (65° 11' N, 147° 52' W, elevation 490-550 m). There were 7 experimental burns, each approximately 2 ha in size. The burns were ignited on different days in July and August of 1978, and varied in the level of burn severity (Dyrness and Norum, 1983). Pre-fire vegetation in these plots was largely black spruce, but some sites had a small component of aspen or paper birch.

Post-fire vegetation changes at the Wickersham sites were monitored in a grid of 20 sample points laid out at 10-m intervals along 4-5 parallel transects at each site. Seedling counts at each sample point were made in circular, 4 m^2 (114 cm radius) plots marked with a metal stake in the centerpoint. Measurements in the 1971 wildfire were made yearly during the first 10 years after fire, and then again 15 (1986) and 31 (2002) years after fire. The vegetation plots in the seven 1978 experimental burns were measured annually during the first three years after fire, and then were not measured again until 2002, 24 years after fire. Measurements of the Wickersham plots prior to 2002 were conducted by the Institute of Northern Forestry at the University of Alaska.

Statistical analysis

Only summary data tables were available for the first three years of observations in the SE Yukon plots, so we did not perform any statistical analyses on data collected during that period. The SE Yukon dataset was also missing data for year 10 in four plots at the Fireside Burn. These plots were excluded from any of time series or pair-wise

analyses that include data from year 10. We confined our analyses of establishment patterns to plots that reached counts of >4 stems of a given species on at least one sample date. Analyses of the SE Yukon data were performed using total stem counts or average cover values across the four sub-plots. Analyses of the Wickersham Dome data were performed using means from the 20, 4-m^2 plots within a site.

The distributions of stem count data for each species tended to be highly skewed with large outliers, and we were frequently unable to transform these data so that they met the assumptions of parametric statistics. In addition, some of our datasets had small sample sizes for which it was difficult to assess departures from normality or homoskedasticity. Given these conditions, we chose to use non-parametric tests for our statistical analyses (Potvin and Roff, 1993; Conover, 1999). Data presented in figures represent the original data, which were then rank-transformed for statistical tests. We used Wilcoxon signed-ranks tests (equivalent to paired *t*-tests) to test for significant positive or negative changes in species density between measurement years 10 and 19. Thinning was estimated as the absolute change in stem counts between years 10 and 19. We used Spearman rank correlation coefficients to test for correlations between data series. In order to compare patterns of net establishment or mortality across species and plots, we standardized tree seedling counts at each measurement date by dividing the observed value by maximum count observed in that plot over the entire record. In this study, 'net establishment' refers to the period or amount of population growth occurring between the disturbance event and the point of maximum population density, while 'net

mortality' indicates a period or amout of population decline following the point of maximum density.

Results

In the SE Yukon, maximum stem densities of aspen, pine and spruce measured within the 20-year observation period spanned three orders of magnitude (Figure 2.1). Pine and spruce densities in individual plots reached over 8 stems per m^2, and aspen densities reached 5 stems per m^2. More commonly, stem densities of 0.5-0.6 stems per m^2 were observed for the three species. In the SE Yukon, stands with high densities of pine tended to also have high densities of spruce (Spearman r=0.54, p=0.0014, n=32), but variations in aspen density were uncorrelated with conifer densities. Mean heights of the three species measured 19 years after fire were 204 ± 26 (mean ± SE), 224 ± 30, and 52 ± 5 cm for aspen, pine, and spruce, respectively. Mean heights within individual plots ranged from 20-650 cm for aspen, 16-686 cm for pine, and 18-126 cm for spruce. Variations in species heights were not correlated with variations in either total tree density or individual species density (p>0.1).

Seedling establishment of pine and aspen in the SE Yukon peaked within 10 years after burning, and reached 50% of the maximum stem counts for those species within 3 years after fire (Figure 2.1). Spruce counts in these plots did not reach 50% of maximum counts until between 5 and 10 years after fire. After the 10-year observation period, densities of pine and aspen declined significantly (Wilcoxon S=-103 and -218.5, p<0.0001, n=25 and 32 for pine and aspen, respectively), indicating the onset of net mortality for these species. In contrast, spruce densities remained constant or increased

slightly during the second decade (S=64.5, p=0.08, n=26). by year 19, aspen stem densities had thinned to a level below that observed in year 5 (S=-144.5, p=0.003, n=32), while pine densities in year 19 were equal to year 5 densities (S=58.5, p=0.095, n=25; Figure 1). Thinning rates of pine and aspen in the second decade after fire were significantly correlated with stem densities of the same species in year 10 (r = 0.81 and 0.78, p<0.001, n=25 and 32 for pine and aspen, respectively), such that the highest mortality rates occurred in plots with the greatest initial densities of that species. Pine and aspen thinning rates were not correlated with percent cover of trees, shrubs or total vegetation, or with stem densities of other species (p>0.1).

In Alaska, maximum stem densities of black spruce at the Wickersham 1971 burn ranged from 1-9 stems per m^2 (Figure 2.2). Black spruce comprised 98% of the post-fire tree seedlings that established at these sites. The highest densities among the 1971 plots occurred in the two low-severity areas containing mature trees that survived the fire. The site with the lowest observed densities (H3) had no surviving trees and was located at a higher elevation on the valley sides than the other four sites, where seed influx rates from uphill areas would have been smaller. Averaged establishment patterns in the Wickersham 1971 burn sites showed that 50% of the net spruce establishment occurred within three years after fire (Figure 2.2). Many of the sites experienced a sharp decrease in stem counts in the fourth year, followed by a period of continued net establishment until approximately 10 years after fire. After 10 years, spruce densities remained nearly constant for the following two decades. Mean spruce heights measured 31 years after fire in the 1971 burn were 60 ± 4 cm (range in plot means 30-106 cm). In the 1978 burn,

mean heights measured 24 years after fire were 56 ± 5 cm (range 34-116 cm) for spruce, 182 ± 19 cm (128-270 cm) for birch, and 82 ± 18 cm (29-154 cm) for aspen. Stem counts in the Wickersham 1978 burns were made too infrequently to estimate the temporal pattern of seedling establishment at those sites.

Within a study area, patterns of relative tree density and composition that were established within a few years after fire remained stable for the duration of the observation periods. In the SE Yukon, rankings of stands based on total tree densities were highly consistent between observations made 5 years after fire and those made 19 years after fire (r=0.86, p<0.0001, n=32; Figure 2.3). This pattern was also true at the species level. Spruce densities measured in year 3 (Wickersham 1978 burns) or year 5 (SE Yukon and Wickersham 1971 burns) were strongly correlated with densities measured 24, 19, or 31 years after fire (r=0.89, 0.92 and 0.81, p=0.007, 0.0001 and 0.10, n=7, 32 and 5, respectively; Figure 2.3). This correlation was only apparent for stands within a study area, as the relative changes in stem densities (equivalent to the slope of the regression line) varied for different sites. The non-significant correlation observed for the Wickersham 1971 burn appears to be more a function of the low sample size (n=5) rather than a weak relationship (Figure 2.3). Patterns of relative species composition observed shortly after fire were also highly consistent with composition patterns observed later in succession (Figure 2.4). For example, the proportion of deciduous individuals within a stand was significantly correlated between years 5 and 19 in the SE Yukon (r=0.95, p<0.0001, n=32) and between years 3 and 24 in the Wickersham 1978 burns

(r=0.82, p=0.02, n=7). The relative proportion of pine *vs.* spruce was also significantly correlated between years 5 and 19 in the SE Yukon (r=0.75, p<0.0001, n=29).

Discussion

The patterns of recruitment that we observed are consistent with data from stand reconstructions that show a large pulse of post-fire tree recruitment followed by several decades of low or no recruitment (Johnson and Fryer, 1989; Sirois and Payette, 1989; Johnson *et al.*, 1994; DesRochers and Gagnon, 1997; Galipeau *et al.*, 1997; Lavoie and Sirois, 1998; Gutsell and Johnson, 2002). Our data support studies indicating that this pulse of post-fire establishment occurs over a period of less than 10 years (Johnson and Fryer, 1989; Lavoie and Sirois, 1998; Gutsell and Johnson, 2002). We suspect that our observations may overestimate the length of the establishment period because of observer error in the detection of very young, small seedlings on the forest floor. In our experience, pine and aspen seedlings are likely to be detected within 2 years after establishment, while spruce seedlings can remain small enough to be overlooked until 3 or 4 years after establishment. Any bias caused by detection limitations would thus have had the greatest effect on our estimates of the timing of spruce establishment.

Previous authors have suggested that variations in the estimated duration of establishment at different sites are related to variations in seed availability or post-fire substrate quality (Foster, 1985; Sirois and Payette, 1989). Our data show little difference in the length of the establishment period between sites located on thick organic layers (20-30 cm) in Alaska and thin organic layers (0-10 cm) or exposed mineral soil in the SE

Yukon. Likewise, the low-severity plots in the Wickersham 1971 burn showed no evidence of an extended establishment period, despite the presence of mature surviving trees that could have provided a local, post-fire seed source. This suggests that the duration of post-fire establishment is limited by post-fire changes in substrate quality, such as moss development or litter accumulation that occur over a similar time frame on both organic and mineral soil substrates. For sites with complete stand mortality, the timing of seedling establishment may be additionally limited by a decline in on-site seed production from serotinous cones of black spruce or pine that occurs within 3-5 years after fire (Zasada, 1986; Sirois, 1995). Further research is needed to determine how changes in post-fire seed availability and substrate quality interact to shape patterns of tree establishment in boreal stands.

The time series data of species density in this study indicate that aspen and pine experience the onset of thinning within the second decade of stand development. Stand reconstructions of lodgepole pine in the Canadian Rockies show a similar onset of thinning in the second or third decade after fire (Johnson and Fryer, 1989). In contrast, our observations of the initiation of aspen thinning after 10 years post-fire conflicts slightly with other studies that show net aspen mortality occurring almost immediately after establishment (Zasada *et al.*, 1992; Greene and Johnson, 1999; Chapter 3). This difference in the timing of mortality may derive from a higher proportion of aspen established from seed (with a slower initial rate of growth) in our plots compared to predominantly asexually-regenerating stands described in the literature (Zasada *et al.*, 1992; Greene and Johnson, 1999; Chapter 3). In many of our plots, there were no

detectable aspen present in pre-fire stands or surroundings (Oswald and Brown, 1990), suggesting that aspen establishment in these plots came from seed. The smaller initial size of seed-originating aspen may allow for a longer growth period before density-dependent thinning starts. However, our mean estimate of aspen density (0.6 ± 0.1 stems/m^2) after 19 years in the SE Yukon is close to the predicted density of 0.9 stems/m^2 obtained from the thinning curve presented by Greene and Johnson (1999) for asexually-produced aspen stems. This similarity suggests that thinning trajectories converge for seed- and sprout-originating stems.

We found that rates of mortality were density-dependent for both aspen and pine, suggesting that self-thinning had been initiated for these species. Thinning rates were positively correlated with initial densities within a species, but not with density or percent cover of trees or shrubs. This pattern indicates that the density-dependence is operating at an intraspecific level even when other species are present in the canopy. Our data indicate that the effects of intra-specific competition on mortality rates are weaker than intra-specific effects, which may be driven by the transmission of species-specific diseases or pathogens. At several of our sites, we noted that dead pines frequently showed evidence of infection by the western gall rust (*Peridermium harknessii* J. P. Moore), an indication that pathogen infection was playing a role in pine mortality. On a species level, the patterns of mortality that we observed generally reflected the expected successional status of the trees at our sites. The two species that commonly dominate early succession (aspen and pine) both showed significant thinning while spruce, which commonly dominates mixed stands only in late succession (Van Cleve and Viereck, 1981), showed no net

mortality during the observation period. This pattern supports the assertion that observed successional dynamics in many boreal forests may be largely driven by differences in mortality rates among species (Gutsell and Johnson, 2002).

The strong correlations that we observed between species densities measured a few years after fire and those measured two or three decades after fire support the hypothesis that early patterns of tree establishment are a strong driver of stand structure (Sirois and Payette, 1989). Although we observed periods of both net population growth and decline in our measurements, relative patterns of species density or composition within a study area were maintained over time. This high level of temporal autocorrelation in stand structure suggests that patterns of future stand composition may be predicted from observations made early in the succession process. Stand reconstructions have shown that continued low levels of tree establishment may occur as a stand ages (Carleton, 1982; Johnson and Fryer, 1989; Sirois and Payette, 1989; Johnson *et al.*, 1994; Gutsell and Johnson, 2002), but these later cohorts also experience high rates of mortality (Johnson and Fryer, 1989; Johnson *et al.*, 1994). As a result, detailed stand reconstructions generally indicate that it is the early post-fire cohorts that dominate the canopies of mature stands (Johnson and Fryer, 1989; Johnson *et al.*, 1994; DesRochers and Gagnon, 1997; Lavoie and Sirois, 1998; Gutsell and Johnson, 2002). Successional changes in canopy composition thus appear to arise due to species differences in growth rates and mortality, rather than differences in the timing of establishment (Gutsell and Johnson, 2002; however, see Galipeau *et al.*, 1997; Bergeron, 2000 for exceptions in the case of balsam fir (*Abies balsamifera* (L.) Mill.)). Given these successional dynamics,

factors that affect post-disturbance recruitment should be expected to play a central role in driving landscape patterns of boreal forest vegetation. As a result, monitoring and manipulation of early seedling establishment patterns may provide powerful tools for applied management of boreal forest stands.

In conclusion, this study has provided additional, independent support for the generalization that the majority of boreal tree recruitment occurs within a short, 3-10 year, period after fire. Repeated seedling counts have shown that density-dependent thinning of the faster-growing species may be initiated within the second decade after fire. Despite the early onset of mortality, patterns of stand density and composition observed within 5 years after fire strongly predict patterns observed 2 or 3 decades after fire. This suggests that landscape variations in forest composition will be strongly influenced by factors that affect post-fire recruitment, and that observations of early establishment patterns are likely to provide powerful insights into future stand development.

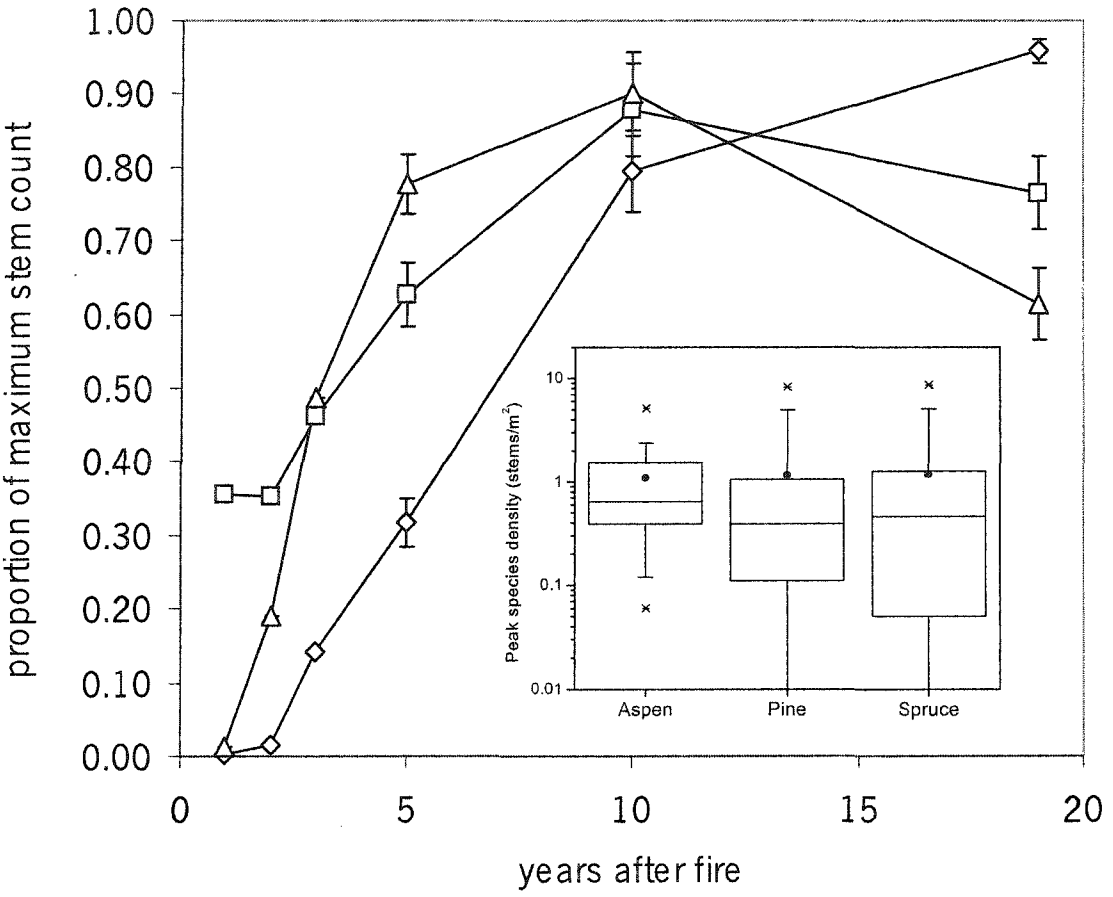

Figure 2.1: Patterns of seedling establishment after fire in the SE Yukon plots. The main graph shows the mean (± 1 SE) proportion of aspen (triangles), pine (squares) or black and white spruce (diamonds) stems established at a given time point, standardized relative to the maximum observed density in each plot. Boxplots (insert) show the distribution of maximum observed densities of aspen, pine, and spruce from the 36 permanent plots. Note the logarithmic y-axis scale. Within the boxes, the sample median is designated as a horizontal line inside the box, and sample mean is shown as a black circle. Bars extending from the box encompass 95% of the observations, and additional ticks show extreme observations.

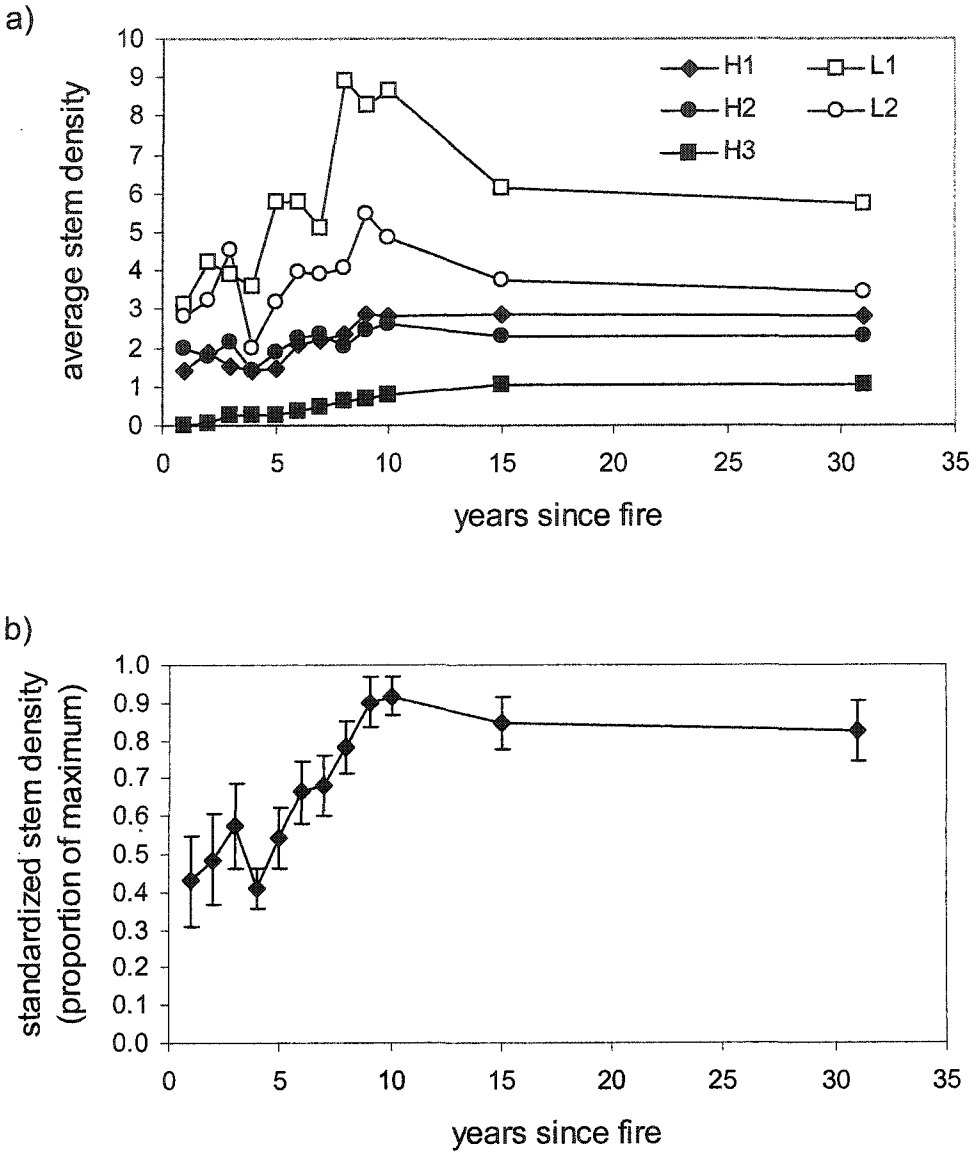

Figure 2.2: Black spruce seedling establishment over time following the 1971 Wickersham fire. Panel (a) shows seedling counts for each plot individually, and (b) gives mean (± 1 SE) seedling counts standardized to the maximum density observed in each plot. Plots H1-H3 are high severity plots with complete stand mortality and L1-L2 are low severity plots with some surviving trees.

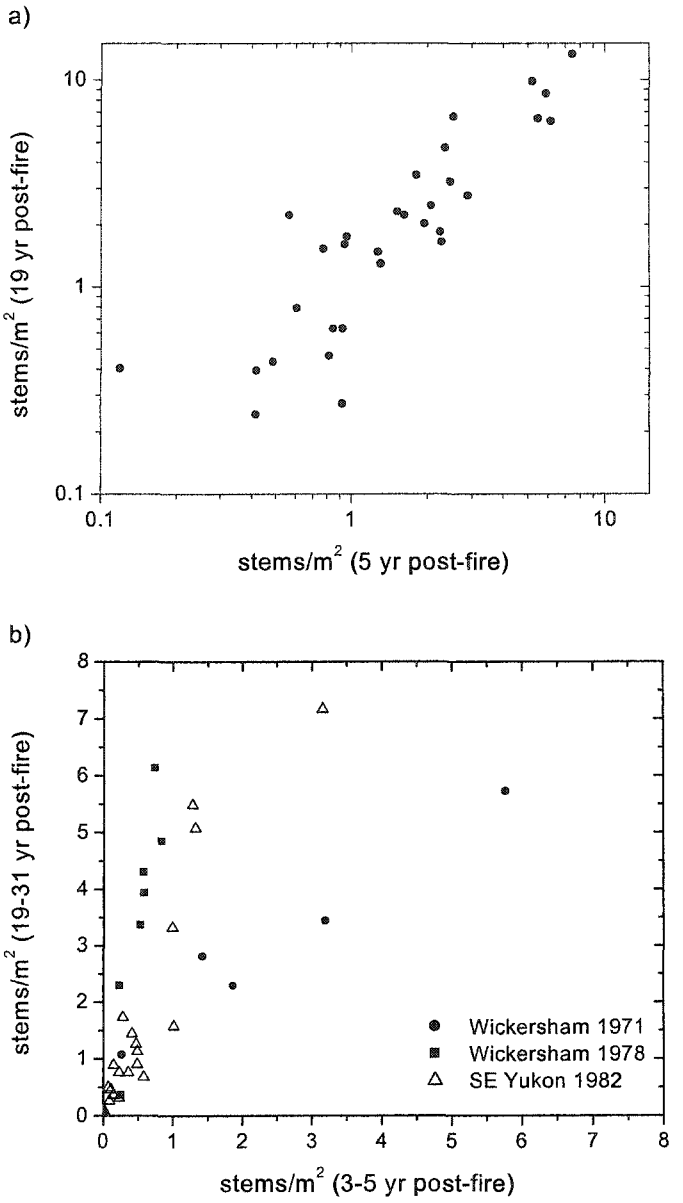

Figure 2.3: Relationships between early and late post-fire measurements of tree densities. Panel (a) shows total stem density measured in the SE Yukon burns in year 5 and year 19 post-fire. Panel (b) shows spruce (black and white pooled) stem density measured in the SE Yukon 1982 burns (year 5 and 19), Wickersham 1971 burn (year 5 and 34), and Wickersham 1978 burns (year 3 and 24). Note the logarithmic axes in panel a.

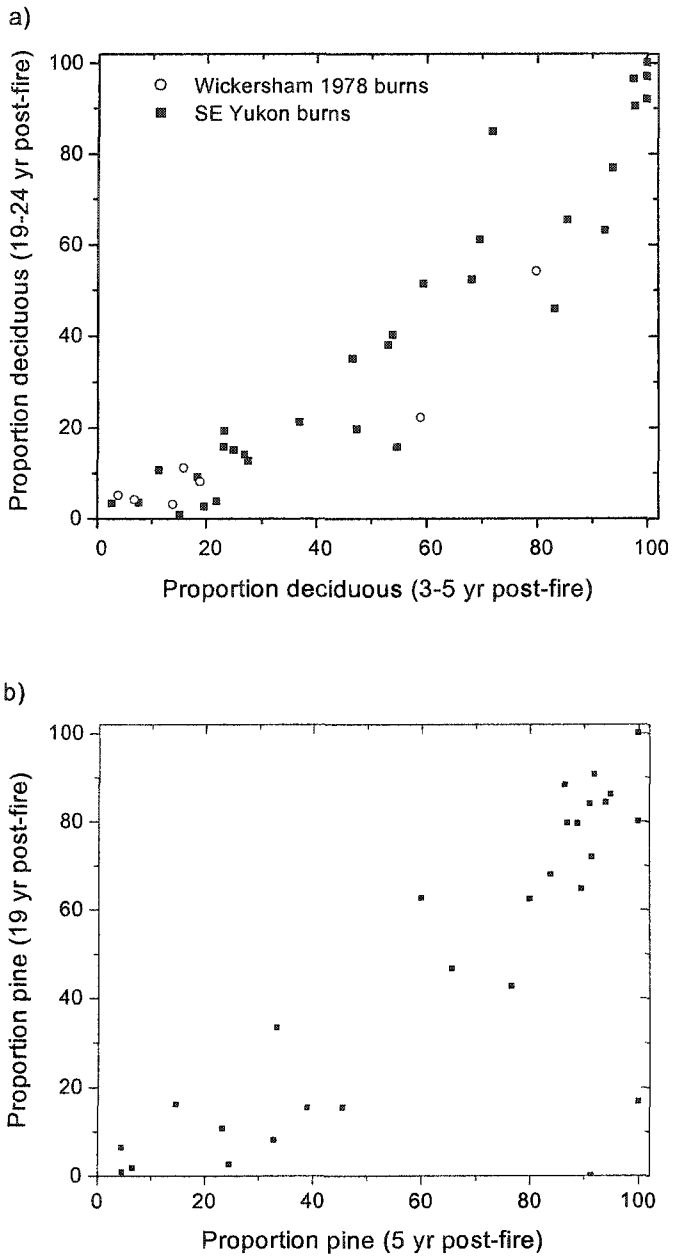

Figure 2.4: Relationships between early and late post-fire measurements of tree composition. Panel (a) shows deciduous stems as a proportion of total trees in the SE Yukon 1982 burns (solid squares; year 5 and 19 post-fire) and Wickersham 1978 burns (open circles, year 3 and 24). Panel (b) shows pine stems as a proportion of total conifers in the SE Yukon burns (year 5 and 19).

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CHAPTER 3: EFFECTS OF ASPEN COMPETITION ON CONIFER RECRUITMENT*

* Manuscript title: Do regenerating aspen stands resist invasion by conifers after fire? Author: J. F. Johnstone. Submitted to Canadian Journal of Forest Research.

Abstract

This experiment was designed to test whether aspen (*Populus tremuloides* Michx.) stands undergoing asexual regeneration after fire are likely to resist post-fire conifer invasion through negative competitive effects on establishing seedlings. The experiment was conducted in a one year-old, naturally-burned aspen stand located near Delta Junction in Interior Alaska. Aspen suckers were removed from a series of experimental plots by repeated clipping of above-ground stems, and the responses of four seeded and transplanted tree species were monitored. Overall rates of establishment of black spruce (*Picea mariana* (Mill.) B.S.P.) and white spruce (*Picea glauca* (Moench) Voss s.l.) at the site were very low, decreasing the power of the experiment to detect the response of spruce to aspen removal. Lodgepole pine (*Pinus contorta* Dougl. ex. Loud. ssp. *latifolia* (Engelm.) Critchfield), the one species with widespread germination, significantly increased seedling establishment rates when aspen was removed. Transplants of aspen, pine, black spruce and white spruce all grew more rapidly when aspen was removed. Results from the experiment indicate that competition by aspen early after disturbance is likely to reduce establishment and growth conifer species; this would prolong the period of deciduous dominance in asexually-regenerating aspen stands.

Introduction

Several studies have demonstrated a negative effect of herbaceous or deciduous plant competition on conifer seedling growth in the boreal forest (*e.g.* Farmer *et al.*, 1988; Morris and MacDonald, 1991; Jobidon, 1994; Bell *et al.*, 2000; Cater and Chapin, 2000; Hangs *et al.*, 2002). Research on this topic has focused on forestry applications, with an aim to provide information on the timing and mechanisms of competitive effects that can be used to develop management options for reducing competition and increasing conifer yield. Much of the research has used transplanted seedlings as the experimental subjects, grown in controlled environments (Farmer *et al.*, 1988; Bell *et al.*, 2000; Hangs *et al.*, 2002), or in conjunction with silvicultural manipulations (Eis, 1981; DeLong, 2000). Although this research has documented the negative effects of light competition on young conifer growth, it has provided relatively little information on the effect of competition in structuring natural forest communities (however see Cater and Chapin, 2000).

The present study focuses on understanding how competitive interactions between asexually-regenerating deciduous trees and sexually-regenerating conifer trees may affect long-term patterns of stand composition following fire in boreal forest. Many common deciduous species in the boreal forest, such as aspen or poplar (*Populus* spp.) and birch (*Betula* spp.) have the capacity to re-sprout from stumps or roots following disturbance (Zasada *et al.*, 1992). This regeneration strategy allows deciduous trees to regenerate and grow rapidly after disturbance by drawing on the belowground resources of pre-disturbance adults. Regeneration by this method would be expected to confer a

competitive advantage over conifer species, such as spruce (*Picea*), pine (*Pinus*) or fir (*Abies*), that must regenerate by seed and depend on limited seed reserves for early growth (Zasada *et al.*, 1992; Greene *et al.*, 1999). In boreal forest, trees that establish within a decade after disturbance frequently account for the majority of canopy trees that occur in a stand (Johnson *et al.*, 1994; Lavoie and Sirois, 1998; Gutsell and Johnson, 2002). As a result, competitive interactions that affect rates of establishment or survival among species early in succession could have long-term impacts on stand development. In mixed-wood habitats of the boreal forest, conifer recruitment in the deciduous understory is frequently limited by low availability of suitable microsites (Simard *et al.*, 1998; Purdy *et al.*, 2002). Where conifers fail to establish, deciduous stands can maintain themselves through gap regeneration (Cumming *et al.*, 2000). Thus, the relative success of conifer recruitment after fire may determine whether stands follow a succession trajectory that leads to conifer or deciduous dominance at maturity. A remaining uncertainty is the extent to which the long-term maintenance of natural, deciduous-dominated stands depends on factors limiting the availability of conifer seed, versus a resistance to conifer invasion caused by negative effects of deciduous competition.

In this research, I address the general question of whether asexual stem regeneration of trembling aspen (*Populus tremuloides* Michx.) reduces rates of conifer establishment and growth during the initial years following fire. The study focuses on aspen because this species is both a prolific re-sprouter and a common stand dominant throughout the boreal forest of North America (Rowe, 1972; Peterson and Peterson, 1992). The study is based on experimental removal of aspen resprouts, and was carried

out under natural conditions in a burned aspen stand with healthy asexual regeneration. The study contributes to our understanding of whether competitive interactions between tree seedlings are likely to help maintain deciduous stands across disturbance cycles by reducing the potential for successful conifer establishment.

Methods

The study area was located on a flat, glacial outwash plain north of the Alaska Range near the town of Delta Junction, Alaska (63° 55' N, 145° 44' W). The vegetation of the area was predominantly open black spruce woodland, with occasional inclusions of aspen-dominated forest. Soils at the study site were coarse and well-drained, consisting of a shallow layer of loess-deposited silt (0-15 cm) on top of alluvial cobbles and gravels. Climate normals in the area indicate a mean summer temperature of 14.1 °C and total summer precipitation of 16.7 cm (NOAA, 2003).

A large, human-initiated fire burned through the area in June and July of 1999. This high-intensity crown fire killed most trees within the burn, and all trees in the area of the study site. The study site was located in a small (~2-4 ha) patch of forest that was dominated by aspen prior to burning. The stand also included small components (<10% of total stems) of balsam poplar (*Populus balsamifera* L. ssp. *balsamifera*), black spruce (*Picea mariana* (Mill.), and white spruce (*Picea glauca* (Moench) Voss s.l.). Most of the surrounding area was dominated by 70 year-old black spruce forest prior to the fire, although there were several other aspen-dominated patches in the vicinity.

The experiment was initiated in June 2000, one year after burning. A total of 32 circular, 2-m diameter plots were randomly located along a 10-m wide band within the aspen patch. The original experimental design also included an artificial warming treatment, and aspen removal and warming treatments were randomly assigned to the plots in a 2x3 factorial design (2 removal levels x 3 warming levels), with 6 replicates for each treatment. The warming factor included 3 treatment levels: greenhouse application, control, and a fenced procedural control designed to mimic the exclosure effects of the greenhouses without an effect on microclimate. The greenhouse treatment used an open-topped design that warmed air temperatures primarily by increasing the height of the soil surface boundary layer (Marion *et al.*, 1997). However, aspen sprouts over-topped the 0.5 m-high greenhouses within the first growing season, reducing or eliminating their boundary-layer effect. Temperature measurements in the second year of the experiment, taken with shielded thermocouples at 5cm above the ground surface, indicated no effect of greenhouses on daily mean or maximum air temperatures ($p>0.1$; data not shown). Likewise, both the greenhouses and procedural controls had no effect on the frequency or intensity of herbivory, which was primarily caused by moose and leaf-eating insects. As a result, the warming treatment was discontinued at the end of the second year, leaving 18 plots assigned to each of the aspen removal and control treatments.

The aspen-removal treatment consisted of aboveground clipping of all aspen stems, contrasted with a control treatment in which the aspen stems were left intact. Balsam poplar sprouts, which were present in low density in 8 of the 36 plots, were treated the same as aspen. Aspen stems were clipped twice in the first growing season, and once in the second and third growing seasons to maintain the aspen removal treatment. Biomass of the clipped stems was

measured in 2000 and at the final harvest in 2002. The experiment was terminated in August 2002, at the end of the third growing season.

Each experimental plot was divided into 6 sub-plots consisting of equilateral triangles (area = 0.28 m^2) arranged in a hexagon with a 15 cm buffer around the external edge of the main plot. Subplots were randomly assigned to a seedling or control treatment. There were four seedling treatments that differed in the species applied: black spruce (BS), white spruce (WS), lodgepole pine (LP; *Pinus contorta* Dougl. ex. Loud. ssp. *latifolia* (Engelm.) Critchfield), trembling aspen (TA), and two unplanted control treatments. Soil samples and other destructive activities were assigned to one of the control sub-plots, while the other subplot was reserved for non-destructive monitoring of natural seedling establishment. Observations during the experiment indicated that naturally-recruited seedlings contributed an estimated 13% (0.2/1.5 seedlings/m^2) of black spruce establishment and 8% (0.2/2.4 seedlings/m^2) of white spruce establishment observed in the seeded plots.

Seeds of black spruce, white spruce, and lodgepole pine were sown into their respective subplots in late June and early September 2000. Aspen was not seeded because of the difficulty in distinguishing between germinating seedlings and re-sprouting shoots. Each seed application consisted of ~0.2 g (0.17, 0.23, and 0.24 g for BS, WS, and LP, respectively) of viable seed scattered on the ground surface within the appropriate subplot. Because seed size varied among the three species, this application rate translated into 472, 317, and 283 viable seeds/m^2 for BS, WS, and LP, respectively. Seed viability was tested on moist filter paper in petri dishes that were monitored over 20 days in a laboratory at 20 °C. The viability trial was conducted in October

2000, and used 5 replicate samples, each of ~100 seeds. Black spruce and white spruce seeds were collected near Delta Junction and Tok, Alaska, and lodgepole pine seeds were collected near Whitehorse, Yukon Territory. Seeds were stored in the freezer prior to use.

In order to separate treatment effects on growth versus establishment, in 2001 I planted established seedlings of black spruce, white spruce, pine and aspen into the same sub-plots (3 seedlings/sub-plot) in which seed of each species had been sown in the previous year. Conifer seedlings were grown from the same seed stock used in the field applications, and aspen seedlings were grown from seed collected near the study site in 2000. Individual seedlings were grown in a sterile peat and vermiculite potting mixture in standard, 4 cm diameter forestry containers for 4 months in a greenhouse at the University of Alaska. Aspen seedlings were started one month later than the conifers in an effort to obtain seedlings of approximately the same size for transplanting. While in the greenhouse, seedlings were watered and fertilized with a 15-30-15 NPK nutrient solution as needed to maintain healthy plants. Temperatures in the greenhouse averaged 22 °C with 20 hours of light in the day. At the time of planting in June 2001, the seedlings were the size of healthy, 2 or 3 year-old natural seedlings. Eight individuals of each species (12 for TA) were randomly harvested prior to transplanting to estimate the average starting biomass for each species. Seedlings that died within the first month after transplanting (12, 3, 1, and 25% of total individuals of BS, WS, LP and TA, respectively) were replaced with new individuals from the same greenhouse stock. I observed fungal hyphae and nodulated roots on many seedlings, suggesting that the seedlings were colonized by mycorrhizae at the time of transplanting.

Vegetation cover and the germination and survival of sown seeds or seedlings were monitored over the summers of 2000, 2001, and 2002. At peak season (late July) in each year, visual estimates of species cover were made in a 1x1 m quadrat positioned in the center of each plot. Cover values for individual species were pooled into growth form classes of herbs (all non-woody dicots plus spore-producing plants), graminoids, shrubs (deciduous and evergreen), and mosses. Plots were surveyed for established seedlings at the beginning, middle and end of each summer. Seedlings were individually marked with color-coded paper clips to identify the year in which they were first observed. Natural establishment rates were estimated from seedling counts in control plots. Because there was no local source of pine seed, spread of planted seedings beyond sub-plot boundaries could also be estimated based on the occurrence of LP seedlings outside the LP plot. All seeded and transplanted seedlings were harvested on August 26, 2002. In the laboratory, current-year growth of the transplanted seedlings was separated from the remainder of the aboveground biomass. Current-year biomass of transplants and total aboveground biomass of sown seedlings were dried in a 60 °C oven for 48 hours and then weighed.

In July 2001 and July 2002, soil organic layer depths were measured at one sample point per plot using a 5 cm soil corer. Soil cores were separated into an organic layer portion and the upper 5 cm of mineral soil, which were weighed before and after drying in a 60 °C oven for 48 hours. These weights were used to calculate gravimetric soil moisture for the 2001 and 2002 samples, and volumetric soil moisture for the 2002 samples.

All statistical analyses were performed using SAS v.8.02 (SAS Institute, Cary, N.C.). Significant differences in variable means between treatments were tested using analysis of variance (ANOVA). Because the species treatment in the experimental design constitutes a split-plot, main and interactive effects of the clipping and greenhouse treatments were tested against the main plot error (plots nested within clipping*greenhouse; Cochran and Cox, 1992). Effects involving species were tested against the residual model error. Initial testing indicated no significant main or interactive effects of the greenhouse treatment ($p>0.05$) on any of the vegetation response variables. That treatment was removed from the analyses, leaving an experimental design with only clipping (main plot) and species (split-plot) factors. Treatment effects on cover of vegetation growth forms were tested together in a multivariate analysis of variance (MANOVA), followed by univariate ANOVAs on individual growth forms. Correlations in growth among species, and between growth and other variables were evaluated using Pearson correlation coefficients. Prior to the analyses, biomass data were log-transformed and cover data were square root-transformed to conform to the distribution requirements of parametric analysis.

Analyses of seedling germination rates and sown seedling weights were performed separately for each species because germinating seedlings of each species were distributed independently among plots, making direct comparisons among species problematic. Black and white spruce both had a high frequency of plots with zero germination (Table 3.1). Because of the high frequency of zeros, I used randomization tests to test for differences in germination and net establishment rates of pine and spruce.

The analyses used 5,000 randomizations of the dataset to construct an expected distribution of *t*-statistics, given a null hypothesis of no difference between treatments, which was compared to the observed two-tailed *t*-value. Treatment differences in biomass of sown seedlings were tested using an unbalanced, one-way ANOVA, where plots without germinants were excluded from the analysis. Because of the low sample size of spruce seedlings, black and white spruce were pooled for this test.

Results

When the experiment was initiated in June 2000, aspen stem density averaged 18.2 ± 2.3 (mean ± SE) stems/m^2 across all plots. Aspen stem densities in the control plots decreased during the experiment to a mean of 6.1 ± 0.7 stems/m^2. At the same time, mean aboveground biomass of aspen increased by a factor of 6 from June 2000 to August 2002 (Figure 3.1), and aspen cover increased by 10 percent, from 36 ± 4 percent in 2000 to 46 ± 3 percent in 2002. The aspen-clipping treatment successfully reduced the aboveground aspen biomass in the treated plots (Figure 3.1) but never completely eliminated aspen because of continued re-sprouting from belowground roots. Sprouting vigor was highest in 2000, where a mean of 17.5 ± 3.5 stems/m^2 were clipped in late July, compared to 2002, where 1.5 ± 0.3 stems/m^2 were clipped in treated plots in late August.

Although all growth forms increased in cover over time, a subset of growth forms also increased in cover in response to aspen clipping (MANOVA for overall clipping*year effect, $F=4.12$, $p<0.001$; Figure 3.2). By the end of the experiment, herbaceous species had higher percent cover in aspen-removal plots than in controls

(ANOVA clipping*year effect, F=13.51, p<0.001). Moss cover was higher in aspen removal plots across all years (ANOVA clipping effect, F=5.14, p=0.03). Graminoids and shrubs showed no response to the clipping treatment (p>0.1).

Pine germination and establishment rates were significantly higher in aspen removal plots than in controls (randomization tests t=2.16 and 1.94, p=0.02 and 0.05, respectively; Table 3.1). In contrast, black spruce showed only a marginally significant effect of aspen removal on germination (t=1.80, p=0.06) and no effect on net establishment (t=1.37, p>0.1), and white spruce showed no treatment effects (t=0.87 and –0.33, p>0.4). Overall rates of conifer seedling establishment where low at the site, and live seedlings of black and white spruce were present in only 15 and 25 percent of the plots, respectively, at the end of the experiment (Table 3.1). Rates of natural spruce establishment (species not identified) were also low, averaging 0.2 seedlings/m^2. The low rates of seedling establishment reduced the effective sample size of the experiment, decreasing the power of the experiment to detect treatment effects on spruce recruitment.

Growth of all transplanted species responded similarly to the aspen removal treatment (ANOVA clip effect, F=10.65, p=0.002; clip*species effect, F=0.21, p>0.8). Mean current-year growth was 40% higher in the removal plots compared to controls (Figure 3.3). Although initial transplant weights were similar among species, species differed significantly in their mean rates of production in 2002, with lodgepole pine producing an average of 1.5 grams of new biomass while aspen transplants produced an average of 0.2 grams (ANOVA species effect, F=202.6, p<0.001). There was no evidence of herbivory of transplanted seedlings, except for minor damage (<25% leaf area

affected) to leaves of trembling aspen by leaf-chewing insects (species unidentified). Total aboveground biomass of sown seedlings at the end of the experiment showed a pattern similar to that of transplants, with pine and spruce accumulating significantly more biomass in clipped plots than in controls ($F=8.77$ and 8.87, $p=0.007$ and 0.008 for pine and spruce, respectively; Figure 3.4). Variations in transplant growth were independent of organic layer depth, which averaged 3 cm at the study site (range 0-8 cm). Measurements of organic layer depth and soil moisture in 2001 and 2002 showed no differences between aspen clipping treatments ($p>0.15$).

Discussion

Patterns of asexual aspen regeneration at this site are similar to those observed in post-fire aspen stands elsewhere. The initial aspen stem densities observed here fall in the middle of the ranges reported at sites across North America (Zasada *et al.*, 1992; Lavertu *et al.*, 1994; Greene and Johnson, 1999). Rapid rates of thinning within the first years after disturbance, such as we observed, are also characteristic of asexually-regenerating aspen stands (Pollard, 1971; Zasada *et al.*, 1992; Lavertu *et al.*, 1994; Greene and Johnson, 1999). Thus, the results of this study should be generally applicable to early succession in aspen-dominated stands. Intensive moose browsing occurred at the study site in 2000 and 2001 and may have limited the potential cover and biomass accumulation of asexually-regenerating aspen. However, these effects should result in conservative assessment of the potential effects of aspen competition.

Seedling establishment of lodgepole pine showed a strong positive response to aspen removal, whereas black and white spruce showed no clear response to the aspen treatment. In the case of black and white spruce, however, the overall scarcity of seedlings clearly reduced the power of the experiment to detect treatment effects. Because of the differences in effective sample size, more confidence should be placed in the estimates of treatment effects for pine than black and white spruce. This experiment thus provides evidence for a negative effect of aspen competition on seedling recruitment of lodgepole pine, while effects on spruce recruitment remain uncertain.

All four species of seedlings in this experiment showed reduced growth in the presence of aspen, and this response was consistent between field-germinated and transplanted seedlings. The lack of species differences in growth response to aspen competition implies that seedlings of these species are similar in their requirements for the resources that were co-opted by aspen suckers. Comparable responses of transplanted and field-germinated seedlings also suggest that aspen has a similar effect on seedling growth for the first 1-4 years after germination. Seedling growth patterns provided no evidence for an increased impact of aspen competition on the growth of species considered to be shade-intolerant (pine and aspen) compared to shade-tolerant (spruce; Burns and Honkala, 1990).

Observed growth responses to aspen canopy removal were more likely due to competition for light (Ter-Mikaelian *et al.*, 1999; Lieffers *et al.*, 2002) than for belowground resources, because aspen roots were not severed and roots may have been present that were connected to stems outside the plot (Peterson and Peterson, 1992).

Increases in litter accumulation under aspen stems may have contributed to shading effects by covering low-stature vegetation, such as mosses or young seedlings, at the soil surface. Because herbaceous plants also compete with young tree seedlings (Wagner *et al.*, 1999; Bell *et al.*, 2000), the positive response of mosses and herbaceous plants to aspen removal may have partially offset the effects of aspen removal on tree seedlings. Nonetheless, the increased growth observed for all seedling species in the removal plots demonstrates that the aspen canopy had a stronger effect on seedling growth than did the compensatory growth of herbaceous plants.

Lodgepole pine exhibited both higher growth and establishment rates than black or white spruce in this study. This pattern is consistent with its ability to occupy an early successional niche in many boreal and montane habitats (Wheeler and Critchfield, 1985; Burns and Honkala, 1990), due to its capacity for more rapid initial growth rates than spruce (Eis *et al.*, 1982; Johnson and Fryer, 1989). Lodgepole pine is also commonly found in well-drained habitats (Wheeler and Critchfield, 1985), and the dry condition of the study site may have constrained its growth and establishment less than that of the spruces. The strong performance of lodgepole pine at a site ~800 km beyond the edge of its range in Yukon Territory, Canada, suggests that the absence of pine species in interior Alaska may be more a function of migration constraints than unsuitability of habitat (Chapter 6).

Our results indicate that asexually-regenerating aspen stands may resist invasion by conifers through competitive effects on conifer seedling establishment and growth. Negative effects of aspen competition on seedling establishment rates, as observed for

lodgepole pine, would have a direct effect of reducing potential colonization rates after disturbance. Even where delayed conifer recruitment occurs in the understory, it is the individuals recruited early after fire that compose the canopies of mature stands (Eis *et al.*, 1982; Johnson and Fryer, 1989; Johnson *et al.*, 1994; Galipeau *et al.*, 1997; Gutsell and Johnson, 2002). Thus, competitive effects on early post-fire establishment are likely to have long-term consequences for stand structure. For those seedlings that do become established, reduced growth rates will lengthen the period that conifer seedlings remained in the sub-canopy, with potential impacts on reproductive potential and survival. Other studies have found significant decreases in tree growth associated with canopy composition, but with relatively little consequent effects on survival over a period of five years (Wagner *et al.*, 1999). In the case of aspen stands, however, the density of canopy shading does not peak until 15-20 years after disturbance (Lieffers *et al.*, 2002), resulting in a long period of suppressed growth for understory conifers. Given that mortality is often higher for small individuals in a stand (Johnson and Fryer, 1989; Johnson *et al.*, 1994), it seems likely that conifer survival rates over the first 2 decades after disturbance would be affected by aspen competition. Stands that experience both reduced conifer establishment and reduced conifer growth are also likely to have reduced availability of conifer seed when they burn again. In this manner, the negative effects of aspen competition on conifer establishment and growth may generate reproductive feedbacks that stabilize the composition of deciduous-dominated stands across multiple disturbance cycles.

Table 3.1: Summary of seedling germination across aspen treatments. Shown are the number of plots with germinating seedlings and mean (± 1 SE) seedling germination rates per gram viable seed in control and aspen removal plots. Mean germination rates were calculated including plots with zero seedling counts (n=18). Total germination is the sum of seedlings observed, while net establishment includes only those seedlings that survived to the end of the experiment.

	No. plots w/seedlings		**Seedlings/g viable seed**	
	Control	Removal	Control	Removal
Total germination				
Black spruce	1	6	0.2 ± 0.2	1.4 ± 0.6
White spruce	6	7	1.1 ± 0.4	1.8 ± 0.7
Lodgepole pine	12	16	5.3 ± 1.4	11.9 ± 2.7
Net establishment				
Black spruce	1	4	0.2 ± 0.2	0.9 ± 0.4
White spruce	5	3	0.6 ± 0.2	0.5 ± 0.3
Lodgepole pine	11	16	4.5 ± 1.3	10.5 ± 2.8

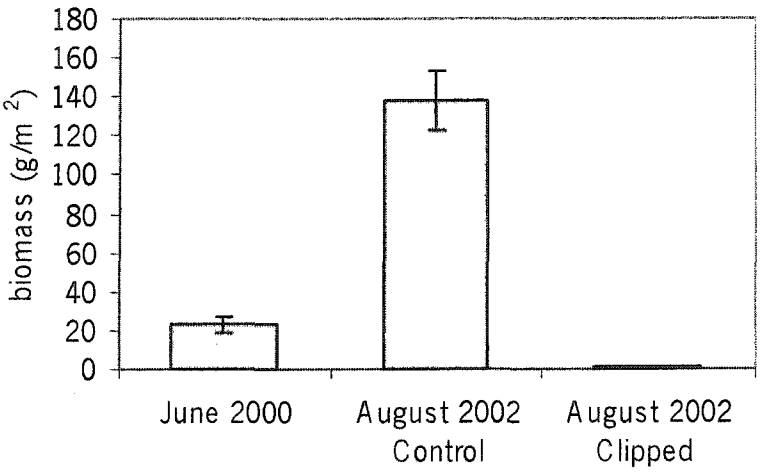

Figure 3.1: Changes in aspen biomass over time and between treatments. Aspen biomass/m^2 (mean ± 1 SE) was measured at the initiation of the experiment in June 2000 (clipped plots, n=18) and at the final harvest in 2002 (n=18 for both control and clipped plots).

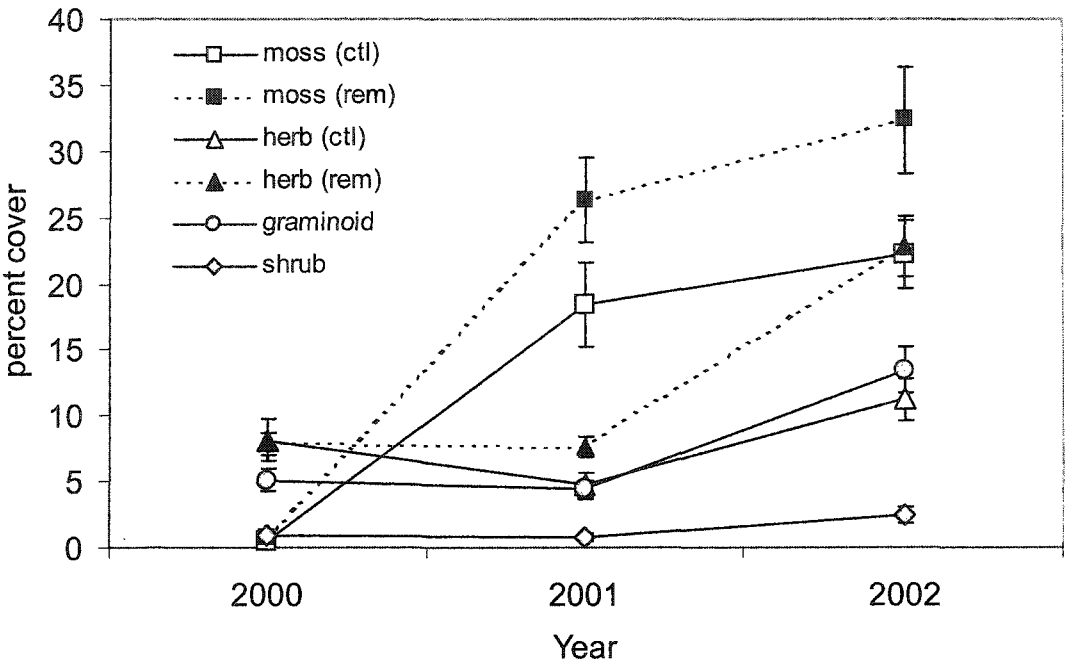

Figure 3.2: Changes in vegetation cover over time. Species cover was summed into growth form classes: mosses (squares), herbs (triangles), graminoids (circles), and shrubs (diamonds). Values (mean ± 1 SE) are shown separately for aspen control (closed symbols) and removal (open symbols) plots for those species groups that showed significant treatment or year*treatment effects. Cover of graminoids and shrubs showed no significant response to the aspen treatment and are represented by means across all plots (grey-filled symbols).

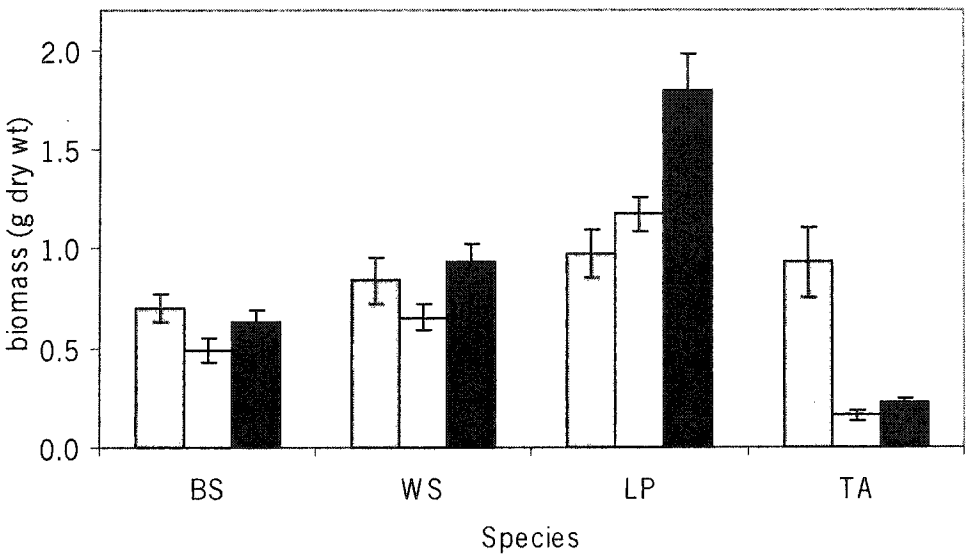

Figure 3.3: Aboveground biomass of transplanted seedlings (mean ± 1 SE). The gray bars show initial transplant biomass at the time of planting in June, 2001. Current-year biomass in 2002 is indicated by white bars for the aspen control treatment and black bars for the removal treatment. Values are shown separately for each species (BS=black spruce, WS=white spruce, LP=lodgepole pine, TA=trembling aspen). Averages are based on individuals (n=8-12) for initial transplant weights, and plot means (n=18) for 2002 biomass production.

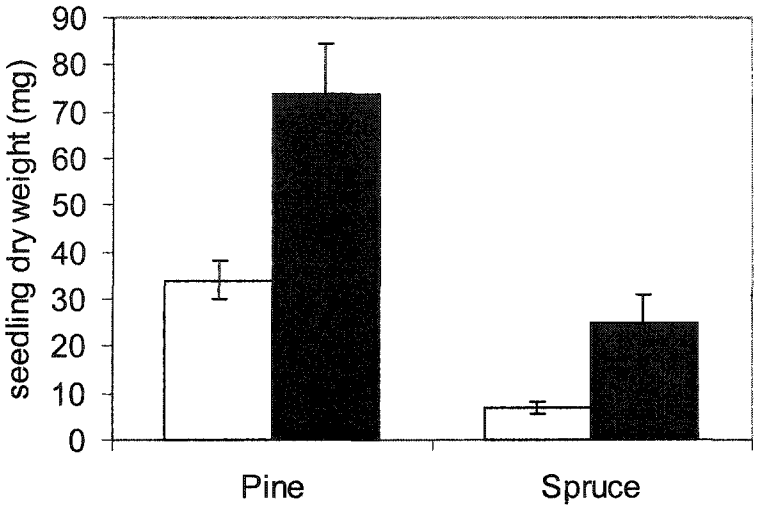

Figure 3.4: Aboveground biomass of field-germinated seedlings (mean ± 1 SE). Control treatments are respresented by white bars and removal treatments by black bars. Values for spruce are pooled for black and white spruce. Averages are based on plot means as replicates, and sample sizes differ across species and treatments (n=11 and 16 for pine and n=9 and 10 for spruce in control and removal plots, respectively).

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CHAPTER 4: EXPERIMENTAL EFFECTS OF BURN SEVERITY*

* Manuscript title: Effects of burn severity on boreal forest structure and composition. Authors: J. F. Johnstone and F. S. Chapin, III. Unsubmitted manuscript.

Abstract

This study examines the effects of burn severity on patterns of post-fire tree establishment in the boreal forest. We present results from 5 separate field experiments examining seedling establishment across different severity levels in 4 burns in central Yukon Territory, Canada, and interior Alaska, USA. The experimental studies focus on the germination, survival, and growth responses of four common tree species, trembling aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*) and black spruce (*Picea mariana*). In all experiments, seedling germination rates were significantly lower on lightly-burned, organic surfaces than on severely-burned surfaces with exposed mineral soil. Severity level had a smaller effect on post-germination survival, and large differences in net establishment between severity levels could be attributed largely to effects on germination. Growth of transplanted seedlings was also significantly reduced on lightly-burned compared to severely-burned soils.

We used a meta-analysis to synthesize the results of our field experiments and test for differences in the magnitude of establishment response to severity levels among species. Overall, we estimated seedling establishment rates to be an order of magnitude less on lightly-burned surfaces compared to severe. Trembling aspen showed a significantly stronger response to burn severity than the conifers, indicating that small-seeded deciduous species may have little potential to establish on organic soils. Among the conifers, lodgepole pine showed a greater relative ability to establish on organic soils than the spruces, and there was no difference in severity response between black and

white spruce. A similar pattern of responses was found in an alternative meta-analysis that included data from our field experiments as well as five other studies from the North American boreal forest. Together, the results of this study indicate that variation in burn severity may have a strong influence on forest community structure, by affecting both the density and composition of tree seedlings that establish after fire. These effects are predicted to be most important in moderately-drained forest stands, where organic material is likely to accumulate but where moisture deficits at the soil surface may also be common.

Introduction

Disturbance is an important driver of variation in community structure and composition in a diverse array of ecosystems (*e.g.* Turner, 1989; van der Maarel, 1993; Moloney and Levin, 1996; Turner *et al.*, 1997; McIntyre *et al.*, 1999). Despite a general acknowledgement of the importance of disturbance in shaping ecosystems, the exact mechanisms by which a disturbance agent acts on community structure are often unclear or poorly described. Increased knowledge of these mechanisms is key to devising effective strategies of ecosystem management and restoration. In addition, a mechanistic understanding of disturbance effects gives us information about the range of ecosystem variation that is possible in a given area, and increases our ability to predict ecosystem responses to future changes in disturbance regime.

The circumpolar boreal forest is an excellent example of the importance of disturbance in driving ecosystem patterns at multiple spatial and temporal scales. Fire is the most common and widespread disturbance agent in the boreal forest (Payette, 1992) and it strongly influences patterns of natural selection (Rowe, 1983; Gauthier *et al.*, 1996), community structure and composition (Van Cleve *et al.*, 1991; Payette, 1992), and landscape pattern configuration (Suffling, 1995; Weir *et al.*, 2000). For example, variations in fire regime contribute to the large variability in post-fire recruitment patterns observed in boreal stands (Zasada *et al.*, 1992; Greene and Johnson, 1999). Stand reconstructions (Johnson and Fryer, 1989; Johnson *et al.*, 1994; Lavoie and Sirois, 1998; Gutsell and Johnson, 2002) and long-term observations (Chapter 2) in boreal forests have

shown that, in most cases, the majority of canopy tree establishment occurs within a short period after fire. As a result, one important mechanism by which fire may influence community structure is by affecting patterns of early establishment. Fire could influence establishment patterns through two primary pathways: a) effects on seed or sprout availability, mediated by fire size and exposure to direct heating or combustion (Rowe, 1983; Schimmel and Granström, 1996; Greene and Johnson, 2000), and b) effects on seed establishment success, mediated by substrate quality (Zasada *et al.*, 1983; Charron and Greene, 2002).

Boreal forests, especially those dominated by conifers, frequently accumulate organic material on the forest floor over time. This accumulation is largely driven by growth of mosses, which contribute to organic accumulation, and cold soils, which limit rates of decomposition (Van Cleve and Viereck, 1981). When a stand burns, this organic layer is burned to varying depths, depending the weather and conditions of the fuel bed (Miyanishi and Johnson, 2002). The amount of organic material that is removed, or the 'severity' of the burn (Rowe, 1983), influences both the availability of propagules stored in the soil (seed and bud banks; Rowe, 1983; Schimmel and Granström, 1996) and the properties of the seedbed available for seed colonization. Although it is generally understood that variations in seedbed quality influence patterns of seedling establishment (Zasada *et al.*, 1992; Greene *et al.*, 1999), studies of the effects of fire severity on seedling establishment have varied in their estimation of the magnitude and direction of these effects (*e.g.*, compare Jarvis, 1966; Sirois, 1993; Duchesne and Sirois, 1995). In addition, many of these studies focus on the establishment of one or two species

(Chrosciewicz, 1974; Sirois, 1993; Duchesne and Sirois, 1995; Herr and Duchesne, 1995), and provide little information on how variations in fire severity may affect patterns of the species composition of the seedling community. Furthermore, because organic layer accumulation varies among communities, the relative importance of burn severity is also likely to vary, but a synthetic assessment of this relationship has not yet been developed.

This study focuses on evaluating the effects of burn severity on patterns of tree seedling establishment in boreal forest. In particular, we asked whether burn severity was likely to have important effects on stand structure and composition of boreal forests, and how those effects were likely to vary among communities within the boreal biome. In this study, a series of field experiments located in different burn areas were used to compare burn severity responses among four common tree species of the boreal forest in western North America, trembling aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*) and black spruce (*Picea mariana*). Data from these experiments allowed us to separate effects of burn severity on establishment into effects on germination, survival and growth. We then used a meta-analysis (Gurevitch *et al.*, 2001) to combine results from these experiments and other published studies to examine the strength of overall severity effects on net seedling establishment, and how effect sizes varied among species and severity levels. Based on these analyses, we propose several hypotheses of how variations in burn severity influence patterns of forest structure and composition.

Methods

Field experiments

Study area

The field results presented here are based on a series of burn severity contrasts made in 4 recently-burned forests of interior Alaska (U.S.A.) and Yukon Territory (Canada; Table 4.1). At the time of burning, each site was vegetated by a mature conifer stand that was dominated by black spruce, white spruce, lodgepole pine, or a mixture of these species (Table 4.1). Sites were selected from the road- or trail-accessible regions of a burn to represent areas of conifer dominance with patches of organic layer remaining intact after the fire. All sites had burned within the preceeding 1-2 growing seasons, and were in the earliest stages of post-fire regeneration. Surviving trees were absent in the vicinity of sites at the CPCRW, Delta, and Fox Lake burns, but there were patches of live trees within 100 m of the study site at the Campbell Highway burn. With the exception of CPCRW, sites were located on flat terrain (Table 4.1). All of the sites were in regions of discontinuous permafrost and are likely to have been underlain by permafrost.

Experimental design

In June 2000, we established burn severity contrasts at each site that compared areas of little consumption of the organic layer (low-severity areas with a portion of the fibric, or upper duff, organic layer intact after the burn) with areas of complete or nearly-complete consumption (severely-burned patches where all of the fibric, and most or all of

the humic organic layers had been burned). Differences among sites in management regulations and soil moisture at the time that experiments were established resulted in slightly different experimental approaches at each site (Table 4.1). At three locations (Delta, Campbell Highway, and Fox Lake) we used natural variations in the depth of burn to establish burn severity contrasts. The sites at Delta and Fox Lake had both experienced patchy smoldering in the organic layer, and we were able to establish interspersed plots located in organic or severely-burned patches. At the Campbell Highway site, we used plots located in adjacent, large patches of severely- or lightly-burned ground to establish the severity contrasts. In all cases, plots were established in an area of visually homogeneous pre-fire tree density and soil conditions. Natural variations in soil burn severity appear to arise from variations in the extent of smoldering combustion during a burn, which are caused by small-scale variations in fuel moisture or fire behavior (Dyrness and Norum, 1983; Miyanishi and Johnson, 2002).

At two additional sites (CPCRW and Fox Lake), we used manual burning of the residual organic layer to establish burn severity contrasts. Plots were located in areas with an intact organic layer, and high and low severity treatments were randomly assigned. For the severe-burn treatment, we used a hand-held propane torch to manually burn away the residual organic layer. Plots assigned to the light-burn (organic) treatment were singed with the propane torch to kill any established above-ground vegetation. The use of both manual and natural comparisons of burn severity levels at the Fox Lake site (plots were established in adjacent areas) allowed us to examine whether vegetation responded similarly to natural and manipulated variations in burn severity.

In addition to the organic and severe burn treatments, three sites had an additional soil treatment in the experiment (Table 4.1). In the Fox Lake natural comparisons, we included an 'ash' treatment, which represented an extreme end of the severity gradient. This treatment consisted of areas in the burn that had been so severely burned that all surface organics, including fine roots and organic carbon in the upper mineral soil, had been completely consumed and nothing but ash and sterile mineral soil were left at the surface. At the Delta site, and in the Fox Lake experimental comparisons, we established a set of plots in which we removed the residual organic layer by hand, rather than by burning. In these plots, we were able to cut through the organic layer around the border of the plot, and peel off the organics with a hoe without disturbing the underlying mineral soil. These plots represented a mineral soil exposure treatment that was similar to the severe burn treatment, but did not include other effects of fire, such as soil heating and deposition of ash and charred organics.

The basic experimental units at each site were rectangular or circular plots split into 5 or 6 smaller subplots. Circular plots were 2 m in diameter and contained 6 triangular subplots (each 0.28 m^2) arranged in a hexagon, surrounded by a 10-15 cm buffer strip along the outside. Rectangular plots were 0.75 m wide and 3.25 m long, and contained 5 triangular subplots (each 0.28 m^2). At several sites, plots were arranged in 2 or 3 blocks that were spatially separated from each other by 10 to 500 m (Table 4.1). Each plot represented a given burn severity level, and species treatments were randomly assigned to subplots in a split-plot design. There were four seedling species treatments: black spruce (BS), white spruce (WS), lodgepole pine (LP), and trembling aspen (TA).

The remaining one or two subplots were unplanted and were used to monitor natural establishment of seedlings.

Seeds of black spruce, white spruce, and lodgepole pine were sown into their respective subplots in late June and early September 2000. Aspen was only seeded in June, within a few weeks of the natural dispersal time for that species. Seeds were applied to the appropriate subplots by scattering seed on the ground surface. Seed provenances came from Delta (BS and TA), Tok (WS), and Whitehorse (LP). The conifer seed had been collected several years previously, while the aspen seed was collected in June 2000. Seed lots of the conifers were stored frozen, and aspen seed at 4 C. Seed viability was tested in the laboratory in May (BS and LP) or September (all species) of 2000. In each viability trial, 4 or 5 replicate samples of ~100 seeds were kept on moist filter paper in petri dishes and hypocotyl emergence was monitored over 2 days (for aspen) or 20 days (for conifers) in a laboratory at 20 C. Seed viability of all species averaged over 70% (Table 4.2). Although similar weights of seed were applied for each species, differences in seed size meant that the numbers of seeds applied varied among species (Table 4.2). Seedling establishment of all species and plots was very low at the site in Delta, and an additional batch of seeds was sown at this site in September 2001. Among all sites, the majority of seedlings germinated in 2000 and 2001, and CPCRW and Delta were the only sites to have new germinants counted in seeded plots in 2002. In plots with high rates of seedling germination, seedlings within a cohort were thinned once to a density of 15 seedlings per sub-plot (~0.5 seedlings/cm^2). Thinning occurred in June 2001 for the 2000 cohort and September 2001 for the 2001 cohort. Estimates of

survivorship of the thinned seedlings were calculated from observed mortality of the remaining seedlings.

In June 2001, young seedlings of black spruce, white spruce, pine and aspen were transplanted into the same sub-plots (3 seedlings/sub-plot) in which seed of each species had been sown. Seedlings were grown for 4 months in a greenhouse at the University of Alaska, from the same seed stock used in the field applications. Seeds were planted in 4x10 cm standard forestry containers (cone-tainers) using a sterile peat and vermiculite potting mixture, and thinned to a single seedling per pot after germination. Aspen seeds were planted one month later than conifer seedlings in an effort to obtain seedlings of approximately the same size for transplanting. Seedlings were watered and fertilized with a 15-30-15 NPK nutrient solution as needed to maintain healthy plants. Temperatures in the greenhouse averaged 22 °C with a 20 hour photoperiod. At the time of planting, the seedlings were the size of healthy, 2 or 3 year-old seedlings grown in a natural environment. Eight individuals of each species (12 for TA) were randomly harvested prior to transplanting to estimate the average starting biomass for each species (Table 4.2). These values were used to standardize measures of current-year production for transplanted seedlings based on the mean starting weight for each species. No seedlings were transplanted into the Fox Lake natural comparison plots, or into mineral soil plots at Delta. In addition, because of mishaps in the transporting of seedlings, no white spruce were transplanted into plots at the Campbell Highway site and six plots at the CPCRW site received only 1-2 aspen transplants/plot.

Field measurements

Vegetation cover and the germination and survival of tree seedlings were monitored over three years. At peak season (mid-late July) in each year, visual estimates of species cover were made in a 1x1 m or 50x50 cm quadrat (for circular and rectangular plots, respectively) positioned in the center of each plot. All sub-plots were surveyed for established seedlings at the beginning, middle and end of each summer. Seedlings were individually marked with color-coded vinyl paper clips or wooden toothpicks to identify the year in which they were first observed. Natural establishment rates were estimated from seedling counts in control plots. All seeded and transplanted seedlings were harvested on August 26, 2002. In the laboratory, current year growth of the transplanted seedlings was separated from the remainder of the aboveground biomass. Current year biomass of transplants and total aboveground biomass of sown seedlings were dried in a 60 °C oven for 48 hours and then weighed.

In July 2002, destructive soil samples were taken from one sample point per plot using a 5 cm soil corer. At sites with circular plots, soil samples were taken from a designated control sub-plot, and at sites with rectangular plots, from a point outside and bordering the triangular plots. Soil cores were separated into an organic layer portion and the upper 5 cm of mineral soil, which were weighed before and after drying in a 60 °C oven for 48 hours to provide information on water content. Bulk density and volumetric water content for the upper 5 cm of soil were calculated as weighted averages of surficial soil layers, based on depths measured in the field. Additional measures of soil organic layer depth were made in 2001 (1 point/plot, 2 cm corer) and at the time of final harvest

in August 2002 (6 points/plot, 5 cm corer). All sample points were averaged together when estimating the organic layer depth of each plot.

Data analysis

We summed all new seedlings observed over the duration of the experiment to estimate the total number of germinated seedlings. In plots that were not burned at the start of the experiment, seedlings that had already established by the June 2000 census were not included in our counts. Survival of germinated seedlings was estimated as the proportion of seedlings alive in August 2002 relative to the number of germinants. Natural seedling establishment, or the number of seedlings surviving to the end of the experiment, was estimated in unseeded control plots, and in seeded subplots of morphologically-distinct species (i.e. natural establishment of black spruce was estimated in seeded plots of aspen and pine, but not in seeded plots of white spruce). Because of the difficulty in distinguishing small seedlings of black and white spruce from each other, we assumed that all control seedlings of spruce belonged to the dominant spruce type at the site (Table 4.1). At sites where there was no local source of pine seed, we estimated seed escapement, or the spread of planted seeds beyond sub-plot boundaries, from the occurrence of pine seedlings outside the designated pine sub-plot. Seed escapement, expressed as the ratio of the number of 'escaped' germinants relative to the number of germinants counted in the seeded sub-plot, averaged 0.020 ± 0.007 (mean $\pm$ SE across sites and treatments, n=11). We used the estimates of pine escapement to correct our estimates of natural establishment of other seeded species. Based on these calculations, natural seedling establishment constituted rarely more than 1%, and never more than 7%,

of the counts obtained in seeded subplots. As the amount of natural establishment (a bias towards increased counts in seeded plots) appeared to be reasonably compensated for by seed escapement (a 2% bias towards decreased counts in seeded plots), we performed our statistical analysis directly on the seedling counts obtained in the field. Establishment responses to burn severity were similar between control and seeded sub-plots, except for a difference in seedling density, so the presence of natural germinants is unlikely to have altered our conclusions about the impact of burn severity on seedling performance.

This study reports on the results of 5 independent experiments, each carried out at a different site, using a common seed source and comparable experimental design. Our approach was to analyze each experiment independently and then compare response patterns across sites as part of the meta-analysis developed in the second half of this paper. The experiment at each site was analyzed as a blocked, split-plot design, where the severity treatment mean square (MS) was tested against the plot MS, and species or species*severity effects were tested against the residual MS (Cochran and Cox, 1992). Severity and species effects were considered to be fixed. In our analysis of seedling survival rates, consistently low germination rates in the organic treatments resulted in many zero values and hindered our ability to test for severity effects on survival within individual sites. As an alternative, we pooled seedlings across plots within a site, and performed an analysis on survival rates using sites as replicates. In order to include the effects of overwintering on survival, only seedlings germinating in 2000 or 2001 were included. Because the Delta site had very few seedlings germinating in 2000-2001, it was not included in the survival analysis. To examine how patterns of cohort survival were

affected by measurement period, we contrasted survival rates measured over a constant period for cohorts and species within one site (Fox Lake Experimental) and treatment (severe). This particular site was selected because its high germination rates provided us with the largest within-plot sample sizes with which to perform our analysis.

Where we performed tests on multiple related variables, such as soil variables or visual cover of vegetation growth forms, we tested for overall treatment effects using a multivariate analysis of variance (MANOVA; Scheiner, 1993). In some cases, we followed a significant MANOVA with univariate ANOVA's, using a Bonferroni-corrected significance level (α/number of tests; Scheiner, 1993), to determine which individual variables showed a significant treatment effect. Our analysis of seedling germination rates was complicated by the use of two standardization methods, using either the weight or number of viable seed sown. We considered both standardization methods to be equally meaningful in a biological sense, although each generated different patterns of responses. To accommodate an analysis of both datasets, we used a MANOVA to estimate overall burn severity effects, and then tested for species main and interactive effects using separate ANOVAs for each standardization method.

Data were examined prior to analysis for outliers, departures from normality or heteroscedasticity of variances, and were transformed where necessary. We used rank transformations in our analysis of germination responses because several sites had large outliers that had a disproportionate effect on the analysis results (Potvin and Roff, 1993; Conover, 1999). Although we applied rank transformations consistently to all germination datasets, in the cases where outliers were not present, an analysis of ranked

data resulted in qualitatively similar results to tests using untransformed data. Survival data were arcsin-transformed prior to analysis. Statistical analyses were performed using SAS (SAS, 2001).

Meta-analysis

Literature review

The overall objective of our meta-analysis was to synthesize existing studies to estimate the effects of burn severity on patterns of net establishment among different boreal tree species. Data for this analysis were obtained from published studies that presented data on tree seedling establishment across different soil burn-severity levels. Our literature review was based on searches in online databases such as OCLC First Search, ISI Current Contents Connect, and ISI Science Citation Index. We used citations in papers from indexed journals to locate studies from the 'grey literature' that were not indexed in journal databases, such as government reports and graduate theses. We restricted our search to studies that a) contained data on seedling establishment for boreal tree species, b) included at least 2 levels of burn severity, and c) were published in English or French. Of the 10 studies we located that fit these criteria, one (Turner *et al.*, 1999) was excluded because data were collected at a site level, rather than the plot level we wished to examine, and two were excluded because seedling data were summarized across substrate types without an explicit treatment of substrate availability (Chrosciewicz, 1974; Zasada, 1985). Finally, two additional studies were excluded because they were not of sufficient duration to include over-winter data on net

establishment (Clautice, 1974; Herr and Duchesne, 1995). Our final meta-analyses were based on data from the experiments presented here, plus five additional studies (Jarvis, 1966; Zasada *et al.*, 1983; Sirois, 1993; Duchesne and Sirois, 1995; Charron and Greene, 2002). These studies included experimental or natural burn severity contrasts at sites in Quebec (Sirois, 1993; Duchesne and Sirois, 1995), Manitoba (Jarvis, 1966), Saskatchewan (Charron and Greene, 2002), and Alaska (Clautice, 1974; Zasada *et al.*, 1983).

Statistical analysis

Because the central questions in this meta-analysis were focused on estimating the relative effect of different post-fire substrate types on establishment success, we chose to calculate effect size as the ratio of establishment on lightly-burned surfaces (the 'treatment') vs. severely-burned surfaces (the 'control'). This metric has been termed the response-ratio (RR) and is generally log-tranformed (ln(RR)) for use in meta-analysis because of the improvement in statistical properties (Hedges *et al.*, 1999; Gurevitch *et al.*, 2001). In this study, values in the numerator (establishment on lightly-burned surfaces) were occasionally zero, making a log-transformation inappropriate. We circumvented this problem by substituting a value equal to the denominator*0.01. Although this procedure is justifiable on the grounds of not excluding reasonable data, it is also important to recognize that such substitutions have the potential to bias estimation of mean effect sizes and confidence intervals.

Most of the published studies we located did not provide sufficient information (mean, variance, and sample size) to enable us to perform the most appropriate type of

meta-analysis, in which samples from studies are weighted based on their variance (Hedges *et al.*, 1999; Gurevitch *et al.*, 2001). Rigid adherence to this method would have eliminated most of the studies from our pool, making a quantitative synthesis impossible. On the grounds that 'some information is better than no information' (Gurevitch *et al.*, 2001), we compromised by performing two sets of meta-analyses, one properly weighted and based solely on the experimental data presented in this study, and another, alternative analysis that included all data that were available. The variance-weighted analysis of our study was based on average net establishment of each species, measured at the end of the experiments, with the sample size equal to the number of plots in each site. The alternative, cross-study analysis calculated response ratios from data on net seedling establishment in the form of totals, averages, or proportions of sown seed, depending on information available from the study. Because we expected studies that included large numbers of seedlings to provide a more precise estimate of severity effects than studies with few seedlings, we used the log of the total number of seedlings as a weighting factor in the meta-analysis. This is analogous to the rationale behind the use of a variance-weighted meta-analysis (Hedges *et al.*, 1999; Gurevitch *et al.*, 2001). We excluded any samples that were based on fewer than 10 seedlings and, consequently, data from our experiment in Delta were not included in either of the meta-analyses.

Each study provided a minimum of one sample for the meta-analysis. As the responses of different species within a study were expected to be independent of each other, each species within an experiment was recorded as an individual sample. Likewise, studies that included data on more than one independent experiment (such as this one)

contributed additional samples. For the cross-study analysis, two types of response-ratios were calculated, one that compared lightly-burned surfaces (usually fibric or dead moss) to severely-burned surfaces (exposed humic or mineral soil), and another that compared severely-burned organic soil (humic) to severely-burned mineral soil. The overall effect size for the humic vs. mineral was estimated only once; all other effect size comparisons were made using response ratios calculated from ratios of lightly- vs. severely-burned surfaces. Details of the data used in the cross-study analysis are given in Tables 4.3 and 4.4.

We used nested categorical analyses to examine overall severity effects and differences in responses among growth forms and species. All models were considered fixed. In the variance-weighted analysis, we first tested for overall severity effects across all species, and then compared estimates between deciduous and coniferous trees, and between lodgepole pine, black spruce and white spruce. In the cross-study analysis, the test for overall effects was followed by comparisons between deciduous and coniferous trees, and between pine (lodgepole + jack) and spruce (black + white). We also estimated the overall effect sizes for responses calculated from humic vs. mineral soil. For all analyses, differences between categories were estimated to be significant when 95% confidence intervals did not overlap. Confidence intervals were estimated using a bootstrap procedure with 999 iterations. We performed our analyses with the program MetaWin (Rosenberg *et al.*, 2000).

Results

Field experiments

In this study, contrasts between high and low burn severity were based on differences in residual organic soil depth, and corresponding differences in the type of soil exposed at the soil surface (Table 4.5). Low-severity burns tended to have thick organic layers and low bulk densities with surface material composed of dead moss or the fibric portion of the organic layer. In contrast, severe burns exposed deeper and denser humic portions of the organic layer, or mineral soil. These differences in surficial soil characteristics were significant at all sites (MANOVA's by site, $p<0.01$). Severely-burned plots always had significantly shallower organic layer depths than organic plots, with mean differences ranging between 3.5 and 7.5 cm of organic material. Organic layer depths within the severely burn plots were generally comparable to those in manually-exposed, mineral soil plots. The trend towards greater organic depths in severely-burned vs. mineral plots reflects the tendency for burned plots to retain a thin residual layer of humic material or charred organics. This was true for the majority of plots we examined except for the very severely-burned, ash plots in the Fox Lake natural comparisons.

Differences in organic layer depths also translated into differences in bulk density (g dry soil/cm^3) and volumetric soil moisture (cm^3 water/cm^3 soil) of the upper 5 cm of soil. The upper 5 cm of soil in organic plots was generally less dense and drier than in severely-burned plots (Table 4.5). Although soil moisture was measured only once, we expect these differences to be generally representative of summer conditions in the plots.

The natural regeneration of different vegetation growth forms responded both positively and negatively to increased burn severity or mineral soil treatments, with the strongest and most consistent response being an increase in moss cover in severely-burned or mineral soil plots (Figure 1). Evergreen shrub and graminoid cover was significantly higher in organic plots at the Campbell Highway and Delta sites, respectively (univariate Anova, $p<0.01$). Although herbs were relatively abundant at most sites, herbaceous cover showed a significant response to severity level only at the Campbell Highway site, where herb cover (dominated by fireweed, *Epilobium angustifolium*) was higher in severely-burned plots (Figure 1). Total vascular plant cover (mosses excluded) was approximately 10 times higher in organic than severe plots at the Campbell Highway and Delta sites, but was similar across severity levels at the other three sites.

Overall seedling germination rates were significantly higher on severely burned vs. organic plots at all sites (Figure 4.2 and 4.3; Table 4.6). Germination on manully exposed, mineral soil surfaces at Fox Experimental and Delta was significantly higher than on severely-burned surfaces, indicating that the effects of a severe burn were not equivalent to the soil removal treatment. There was, however, no significant difference in germination on ash vs. severely-burned surfaces at the Fox Natural site (Table 4.6).

Patterns of overall germination rates and responses to severity among species depended on how germination counts were standardized. When germination rates were expressed on a per g seed basis, species frequently overlapped in their mean germination rates, and patterns were generally site-specific (Figure 4.2). At the Campbell Highway

and Fox Experimental sites, aspen showed a stronger response to severity level than did the other species (species*severity effect, $p<0.01$), having one order of magnitude higher germination rates (per gram seed) in severely-burn plots than other species (Figure 4.2). However, when germination rates were expressed based on numbers of sown seeds, aspen germination rates frequently fell below those of the conifers, especially lodgepole pine and black spruce (Figure 4.3). Germination rates (per 100 sown seeds) of lodgepole pine in organic plots were frequently higher than for the other species, although this pattern was statistically significant only at the Fox Lake Experimental site (Figure 4.3).

Compared to effects on germination, burn severity effects on seedling survival were relatively weak, with 10-20% reduction in conifer survival rates in organic plots relative to severely-burned (Figure 4.4; $F_{1,25}=3.56$, $p=0.07$). Across all sites, seedling survival varied significantly among cohorts ($F_{1,25}=10.16$, $p=0.004$), but not among species ($F<0.8$, $p>0.1$ for species main and interaction effects). Among the conifer species, survival rates in the 2000 cohort were 20-40% lower than in the 2001 cohort. However, because of strong treatment effects on seedling germination rates (Figures 4.2 and 4.3), the number of seedlings used in the calculation of survival rates for each site varied substantially between severity treatments (Figure 4.4b). Given the larger number of initial germinants in the severe burn treatment, we expect survival estimates for that treatment to be more robust than for the organic treatment. Trembling aspen was not included in the survival analysis because it was seeded as a single cohort, and low germination rates in organic plots prevented estimating survival across severity treatments. In severely-burned plots, aspen survival averaged 0.16 ± 0.07 (mean $\pm$ SE,

n=4), a value that is substantially lower than the survival rates estimated for conifers in the same plots.

A closer look at seedling survival rates among cohorts, using data from the severely burned plots at the Fox Lake Experimental site, indicates that 2-year survival rates were significantly lower for the 2000 cohort than the 2001 cohort (Figure 4.5, cohort effect $F_{1,28}=28.28$, $p<0.0001$). Differences in cohort survival may be related to differences in the timing of germination (Wang and Lechowicz, 1998). The majority of seeds planted in June 2000 did not germinate until after mid-July of that year, while most seeds planted in September 2000 germinated before mid-July 2001. For all species, the period of greatest mortality for the 2000 cohort occurred during the winter of 2000-2001, while mortality for the 2001 cohort was greatest during summer of 2001. Thus, for both cohorts, the greatest proportional mortality occurred in the months immediately following germination, regardless of whether the season was winter or summer.

Given the small effects of severity treatment on survival, and relatively constant rates of survival among conifers, it is not surprising that patterns of net seedling establishment (total live seedlings at the end of the experiment) closely reflect patterns of initial germination (Figures 4.3 and 4.6). However, net establishment of aspen was low across all treatments, due to effects of low survivorship for this species. The combination of relatively high germination (Figure 4.3) and survivorship (Figure 4.4) of lodgepole pine on organic surfaces compared to other conifers resulted in pine having the highest success rate of establishment on lightly-burned surfaces among the four species studied (Figure 4.6).

Patterns of natural seedling establishment across severity treatments were similar to those observed in seeded plots, although the density of natural seedlings was generally only a small proportion of that observed in sown plots (see Methods). At the CPCRW site, however, we did observe substantial natural establishment of paper birch, *Betula papyrifera*. Birch germination averaged 15.6 ± 5.5 (mean ± SE) seedlings/m^2 in severely-burned plots and 3.9 ± 1.5 seedlings/m^2 in organic plots. The majority of this establishment occurred in the final year of the experiment, so we were not able to estimate over-winter survival rates.

Growth of transplanted seedlings was always higher in severe vs. organic plots, except at the Campbell Highway site, where aspen growth showed no response to the severity treatment (Figure 4.7). The observed pattern of aspen growth at the Campbell Highway site is likely to have been influenced by hare herbivory, as 33% (9/27) and 63% (17/27) of transplanted aspen in the organic and severe plots, respectively, were completely removed by herbivory. Treatment tests were based on the remaining samples, and both reduction of sample size, and partial removal of biomass by herbivores may have confounded our ability to detect a severity response. Current-year growth averaged across treatments was greater for conifers than aspen at all sites (Figure 4.7).

Meta-analysis

The meta-analysis of response-ratios obtained from our experiments indicated a significant and large overall effect of burn severity on seedling establishment (Figure 4.8). The estimated mean ln(RR) across sites and species was –2.54, indicating that overall seedling establishment on lightly burned surfaces was over an order of magnitude

less on lightly-burned compared to severely-burned surfaces. Estimation of separate effect sizes for coniferous and deciduous growth forms indicated that deciduous trees (in this case, trembling aspen) were much more sensitive to severity effects than coniferous trees (lodgepole pine, black spruce, and white spruce). In comparing among conifer species, the estimated effect size was significantly less negative for lodgepole pine than black or white spruce, indicating a lower sensitivity of pine to severity level compared to spruce (Figure 4.8).

Our second, more inclusive meta-analysis of burn severity effects also estimated an overall effect size that was significantly less than zero, supporting observations from our experiments that substantially lower seedling establishment occurs on lightly-burned surfaces (Figure 4.8). In contrast, response-ratios that compared establishment on severely-burned surfaces with exposed humic vs. mineral soil were not significantly different from zero. Thus, at a high severity levels, the presence or absence of a thin organic residue had no consistent effects on seedling establishment. Within the light vs. severe burn comparison, the cross-study meta-analysis showed a similar pattern among growth forms as observed in our experiments, where deciduous species were significantly more sensitive to severity effects than conifers (Figure 4.8). There was also a nonsignificant trend towards reduced sensitivity of pine (jack and lodgepole) compared to spruce (black and white).

Discussion

Patterns and mechanisms of severity response

Results from our field experiments showed a strong and consistent enhancement of the germination, survival, and growth of boreal tree species when burn severity was high. We therefore expect substantially less seedling establishment on organic soils following a low-severity burn compared to one of high severity. Severity effects were probably related to the difference in seedbed quality between surficial organic layers vs. deeper organic or mineral soil layers. In a light burn, the upper dead moss or fibric layer of the soil is not fully combusted, which leaves a porous layer at the soil surface. The low bulk density and open structure of these layers allow greater air flow, more rapid drying, less moisture wicking, and therefore more frequent episodes of drought-stress than in denser layers that remain following more severe fires (Zasada *et al.*, 1983; Steijlen *et al.*, 1995). Dry, low-density surface layers also exhibit greater temperature extremes than a denser, moister soil layer because of their lower thermal heat capacity and less cooling from surface evaporation (Coyea, 1988; Duchesne and Sirois, 1995). In addition, more root growth is required for a seedling to reach a dependable moisture source in a deep vs. shallow organic layer. Seedlings on these substrates are therefore subjected to a greater frequency and intensity of drought- or temperature-stress events during the vulnerable establishment period, when roots have not yet penetrated to deeper soil layers. Lower moisture availability may also reduce the bulk flow of nutrients to seedling roots, reducing growth potential on these substrates. Evidence of increased nutrient stress is

suggested by our observations of a higher frequency of needle chlorosis among conifer transplants located in low-severity compared to high-severity plots (Johnstone, personal observation).

Burn severity also influences revegetation patterns by determining the portion of the seed or bud bank that is destroyed by fire. In two of our experiments, we observed a significantly greater cover of shrubs and graminoids (both composed of re-sprouting species) in the lower severity plots (Figure 4.1). In contrast, high-severity plots had greater cover of wind-dispersed mosses such as *Ceratadon purpureus* and *Polytrichum juniperum*. These patterns are consistent with the prediction that low-severity burns favor re-sprouting vegetation, while high-severity burns favor species that establish by dispersal (Rowe, 1983; Schimmel and Granström, 1996). We found, however, little evidence for positive effects of shelter by resprouting vegetation on seedling establishment in low-severity plots (hypothesized by Thomas and Wein 1985). Most germinating seedlings in the low severity plots occurred in open microsites, such as cracks and hollows, as opposed to sites under the shelter of other vegetation. Any potential positive effects of shelter may have been offset by increased litter accumulation under grasses and shrubs.

Although all four tree species in our experiments showed decreased establishment and growth on the lightly-burned compared to severely-burned substrates, the meta-analysis of our experimental data indicated that burn severity level had a significantly greater relative effect on aspen than on conifer establishment. Aspen seeds are 2 orders of magnitude smaller than those of conifers, which likely accounts for the low rates of aspen

establishment per seed on both organic and mineral soils. Small seeds have fewer reserves to support root growth and thus may experience a longer period in which they are vulnerable to mortality caused by temperature and drought stress. Nevertheless, the high germination rates of aspen (per gram seed) on severely-burned surfaces (Figure 4.2) indicate that small seed size may be partially compensated for by large numbers of seed. Overall survival rates of aspen seedlings were also lower than those of conifers, however, and net seedling establishment of aspen (per gram seed) was lower than the conifers in 3 of the 5 experiments (data not shown). Low aspen establishment was particularly evident on lightly-burned surfaces, where germination of aspen was uniformly poor. The small seed sizes characteristic of deciduous species (Zasada *et al.*, 1992) probably contribute to the greater sensitivity to burn severity of deciduous species revealed in our cross-study meta-analysis (Figure 4.9).

Across our experiments, lodgepole pine showed a trend towards higher establishment on organic soils than did spruce, but this pattern that was frequently non-significant at the level of individual experiment. When the relative severity responses of the species were combined in a single meta-analysis, however, the sensitivity of pine establishment was significantly lower than that of black and white spruce (Figure 7). Our cross-study analysis also indicated a trend toward decreased sensitivity of pine relative to spruce (Figure 4.8), perhaps explaining the capacity of pine to persist and dominate across a wide range of habitat types (Burns and Honkala, 1990). The similarity of seed weights between lodgepole pine and white spruce (Table 4.2), indicate that differences in the amount of seed reserves are unlikely to explain differences in establishment patterns

between the two species. The higher rates of root extension of pine compared to spruce observed in our viability trials (J. Johnstone, personal observation) could contribute to increased establishment rates of pine on stressful sites.

A comparison of severity responses among individual sites demonstrates that the unique conditions of a burn will also influence patterns of seedling responses to severity gradients. At the Delta site, severe burns resulted in the formation of a veneer of aolian-deposited silt at the soil surface, which was perched above a thin layer of charred organics (Table 4.3). Germination on this silt 'veneer' was only slightly greater than on organic surfaces (Figure 4.3), probably because the charr layer isolated the soil surface from wicking of below-ground moisture. Similarly, patterns of net establishment across the Fox Lake natural comparisons indicate that very high levels of burn severity may reduce potential seedling establishment rates (Figure 4.6). Although such burns increase the exposure of mineral soil, they may also negatively affect the structure and nutrient content of the surface soil layers (Dyrness and Norum, 1983; Keays, 1987). At Fox Lake, we found that the mineral soil surface of the 'ash' treatment was a hard crust that largely restricted seedling establishment to cracks in the soil surface. Seedlings that established on this substrate were frequently small and chlorotic, indicating the potential for decreased growth and survival on this substrate relative to severely-burned surfaces that retained a thin layer of humic material. A meta-analysis comparison of seedling establishment on severely-burned soils with a surface layer of humic vs. mineral soil showed no consistent effect of an increase in burn severity, supporting the expectation of

variable effects of severity at the high end of the gradient (Chrosciewicz, 1974; Sirois, 1993).

Severity effects on forest structure and composition

Variations in burn severity may affect stand structure by influencing the density and spatial patterns of seedling establishment. Severe burns are likely to promote dense post-fire tree recruitment, leading to narrowly even-aged stands with high levels of canopy competition. In contrast, light burns will frequently reduce recruitment rates, leading to open tree canopies that permit delayed seedling establishment and the development of multi-aged stands (Foster, 1985). At a local scale, patchiness in burn severity can generate spatial structure in the density and arrangement of established trees. Patchiness in burn severity may also maintain spatial structure over time, as deep burning around the bases of trees (Miyanishi and Johnson, 2002), or mineral soil exposure in tree tip-ups (Clautice, 1974) favor tree establishment in the same microsites occupied by pre-fire individuals. Temporal stability in the spatial structure of vegetation may, in turn, generate spatial structure in the rates and patterns of biogeochemical processes (Pastor *et al.*, 1999).

Species differences in sensitivity of establishment to burn severity can lead to shifts in successional trajectory. Many conifer-dominated stands in the boreal forest are characterized by accumulation of organic material of sufficient depth that severe burns are uncommon (Dyrness and Norum, 1983; Wein, 1983; Miyanishi and Johnson, 2002). Residual organic material remaining after a light or moderate burn at these sites will generally prevent post-fire establishment of deciduous seedlings. Under these conditions,

burns will favor dominance by serotinous conifers, which can provide the large quantities of seed needed to provide successful recruitment on organic soils. Substrate effects on regeneration are thus a likely mechanism contributing to the conifer-to-conifer succession dynamics commonly observed in organic-rich sites (Van Cleve and Viereck, 1981). However, fires that occur under unusually dry conditions at these sites can generate severe burns (Viereck, 1983; Wein, 1983), opening up substrates for establishment by deciduous species or conifers seeding in from outside a burn. Under such conditions, alternative, mixed deciduous/conifer communities can become established that represent a dramatic departure from stable cycles of conifer dominance. Because of negative effects of deciduous cover on moss growth and organic layer accumulation (Oechel and Van Cleve, 1986; Mann and Plug, 1999), initiation of a mixedwood trajectory by a severe burn may alter rates of organic layer accumulation, leading to a shift in the probability of future severe burns. The likelihood of a site returning to a conifer trajectory will be dependent on whether species effects on biogeochemical processes are sufficiently strong to override abiotic controls of these processes.

Variations in site moisture conditions across a landscape will influence rates of organic layer accumulation and the probability of a severe burn, therefore influencing sensitivity of successional trajectories to change. We expect burn severity effects to be most important at moderately-drained sites, where there is the greatest potential for variation in organic layer thickness to affect seedling establishment. At well-drained sites where organic layers are shallow, high severity burns are common (Miyanishi and Johnson, 2002), and seedling establishment is unlikely to be limited by organic layer

accumulation. In poorly-drained sites, abiotic conditions strongly favor organic material accumulation and maintenance of water-logged soil conditions (Trumbore and Harden, 1997). Severe burns in these soils will therefore only occur under extreme weather conditions, and although a severe burn may disrupt moisture and thermal regimes of permafrost soils (Wein, 1983), the strength of abiotic controls at these sites suggest that alterations in succession trajectory are likely to be short-lived (Viereck, 1983).

Changes in climate are likely to influence the frequency of severe burns on a landscape, by altering the weather conditions under which fires burn (Flannigan and Van Wagner, 1991; Stocks *et al.*, 1998), and affecting patterns of organic matter accumulation (McGuire *et al.*, 1995; Trumbore, 1997). These changes will interact with landscape controls over moisture availability to influence boreal ecosystem response to climate change. Changes in the frequency of severe burns are expected to have relatively small impacts on succession patterns in well-drained or poorly-drained sites, where abiotic controls strongly constrain vegetation responses. In contrast, an increased frequency of severe burns at moderately-drained sites could have long-term impacts on forest composition, by initiating alternative succession trajectories with strong feedbacks to the biophysical environment.

Table 4.1: Summary of site characteristics. Details of location, site conditions, and severity treatments are given for the five experimental sites in Alaska (AK) and Yukon Territory (YT).

Site	Location	Burn year and type	Severity treatments	Manipulation	Plot arrangement	Pre-fire composition	Topography and soils
CPCRW[a] (AK)	65 10' N 147 31' W	1999 exp. burn	Organic Severe	Manual burning	circular plots 2 blocks 6 replicates/trmt	Black spruce (100%)	NE slope (3-8), well-drained, silt loam over cobbles
Delta (AK)	63 55' N 145 44' W	1999 wildfire	Organic Severe Mineral	Natural comparisons (interspersed) and manual removal	circular plots 0 blocks 6 replicates/trmt	Black spruce (80%) + white spruce (20%)	Flat, well-drained, silt loam over cobbles
Campbell Highway (YT)	62 07' N 135 17' W	1998 wildfire	Organic Severe	Natural comparisons (contiguous areas)	rectangular plots 3 blocks 9 replicates/trmt	Black spruce (85%) + white spruce (12%) + lodgepole pine (3%)	Shallow W slope (0-3), moderately-drained, sandy loam
Fox Lake, Experimental (YT)	61 19' N 135 36' W	1998 wildfire	Organic Severe Mineral	Manual burning and removal	circular plots 2 blocks 6 replicates/trmt	White spruce (100%)	Flat, moderately-drained, silt loam
Fox Lake, Natural (YT)	61 19' N 135 36' W	1998 wildfire	Organic Severe Ash	Natural comparisons (interspersed)	rectangular plots 2 blocks 6 replicates/trmt	White spruce (100%)	Flat, moderately-drained, silt loam

a Caribou and Poker Creeks Research Watershed (CPCRW) is component of the Bonanza Creek LTER site, and was burned in the Frostfire experimental burn (Hinzman, 2000).

Table 4.2: Details of species seed and transplant applications. Viability rate and transplant biomass are shown as means ± 1 SE (n). Sowing rates are expressed as the weight (g/m^2) and number ($\#/m^2$) of viable seeds sown in a single application. Note that aspen was seeded once, and conifers twice, in plots with an individual area of 0.28 m^2.

	Lodgepole pine	**Black spruce**	**White spruce**	**Trembling aspen**
Viability rate	0.86 ± 0.01 (9)	0.73 ± 0.05 (9)	0.81 ± 0.02 (5)	0.81 ± 0.01 (5)
Viable g/m^2	0.86	0.73	0.81	1.73
Viable seeds/m^2	282	559	316	17060
Transplant biomass (g)	0.70 ± 0.07 (8)	0.84 ± 0.12 (8)	0.98 ± 0.12 (8)	0.93 ± 0.17 (12)

Table 4.3: Studies comparing seedling establishment on lightly-burned organic (fibric) vs. severely-burned mineral or humic soil. A meta-analysis was performed using response ratios weighted by the total number of seedlings recorded (ln(seedl#)).

Publication	Species	Organic	Severe	ln(RR)	ln(seedl#)
Charron and Greene, 2002	Pinus banksiana	4	173	-3.8	5.2
Charron and Greene, 2002	*Pinus banksiana*	3	43	-2.7	6.1
Charron and Greene, 2002	*Picea mariana*	18	454	-3.2	5.3
Charron and Greene, 2002	*Picea mariana*	3	52	-2.9	4.4
Jarvis, 1966	*Pinus banksiana*	1.5	6.1	-1.4	4.2
Jarvis, 1966	*Pinus banksiana*	2	2.3	-0.1	3.9
Jarvis, 1966	*Picea glauca*	0.2	1.5	-2.0	2.7
Jarvis, 1966	*Picea glauca*	0.4	1.3	-1.2	3.0
Sirois, 1993	*Pinus banksiana*	0.02	0.004	1.6	4.9
Sirois, 1993	*Picea mariana*	0.008	0.002	1.4	6.2
Zasada *et al.*, 1983	*Picea mariana*	0.173	17.3	-4.6	3.9
Zasada *et al.*, 1983	*Alnus crispa*	0.17	17	-4.6	4.2
Zasada *et al.*, 1983	*Populus tremuloides*	0.064	6.4	-4.6	4.2
Zasada *et al.*, 1983	*Populus balsamifera*	0.06	6	-4.6	3.7
Zasada *et al.*, 1983	*Salix bebbiana*	0.068	6.8	-4.6	3.8
Zasada *et al.*, 1983	*Salix alaxensis*	0.192	19.2	-4.6	5.2
Zasada *et al.*, 1983	*Betula papyrifera*	3.6	80.8	-3.1	6.3
Zasada *et al.*, 1983	*Salix scouleriana*	0.192	19.2	-4.6	3.7
This paper	*Pinus contorta*	27	56	-0.7	4.4
This paper	*Pinus contorta*	9	68	-2.0	4.3
This paper	*Pinus contorta*	101	214	-0.8	5.8
This paper	*Pinus contorta*	27	85	-1.1	4.7
This paper	*Picea mariana*	6	184	-3.4	5.2
This paper	*Picea mariana*	3	11	-1.3	2.6
This paper	*Picea mariana*	33	403	-2.5	6.1
This paper	*Picea mariana*	22	224	-2.3	5.5
This paper	*Picea glauca*	2	80	-3.7	4.4
This paper	*Picea glauca*	3	17	-1.7	3.0
This paper	*Picea glauca*	10	134	-2.6	5.0
This paper	*Picea glauca*	2	50	-3.2	4.0
This paper	*Populus tremuloides*	10	110	-2.4	4.8
This paper	*Populus tremuloides*	1	43	-3.8	3.8
This paper	*Populus tremuloides*	3	41	-2.6	3.8
This paper	*Populus tremuloides*	1	31	-3.4	3.5
This paper	*Betula papyrifera*	39	155	-1.4	5.3

Table 4.4: Studies comparing seedling establishment on severely-burned organic vs. mineral soil. A meta-analysis was performed using response ratios weighted by the total number of seedlings recorded (ln(seedl#)).

Publication	Species	Severe	Organic	ln(RR)	ln(seedl#)
Charron and Greene, 2002	*Pinus banksiana*	43	91	0.7	4.9
Charron and Greene, 2002	*Picea mariana*	52	66	0.2	4.7
Charron and Greene, 2002	*Picea glauca*	46	86	0.6	6.9
Jarvis, 1966	*Pinus banksiana*	6.1	3.4	-0.6	4.4
Jarvis, 1966	*Picea mariana*	0.5	0.4	-0.2	2.1
Jarvis, 1966	*spruce, white*	1.5	0.4	-1.3	2.8
Duchesne and Sirois, 1995	*Pinus banksiana*	18	4	-1.5	3.1
Duchesne and Sirois, 1995	*Picea mariana*	22	7	-1.1	3.4
Sirois, 1993	*Pinus banksiana*	0.004	0.006	0.4	4.4
Sirois, 1993	*Picea mariana*	0.002	0.002	0.0	5.0
This paper	*Picea mariana*	57	224	1.4	5.6
This paper	*Pinus contorta*	63	85	0.3	5.0
This paper	*Populus tremuloides*	17	31	0.6	3.9
This paper	*Picea glauca*	29	50	0.5	4.4

Table 4.5: Description of soil characteristics among burn severity treatments at 5 sites. Means ± 1 SE are given for the depth of the organic layer (from the organic soil surface to the mineral soil), and bulk density and volumetric water content of the upper 5 cm of soil, including the upper mineral soil in plots with an organic layer <5 cm thick. Estimates of bulk density and water content are from measurements made in mid-July, 2002 (1 sample/plot). Estimates of organic layer depth are based on averages across all soil sampling dates (6-8 samples/plot). Values with different letters represent significant differences between treatments within a site (Tukey's multiple range test, $p<0.05$).

Site/Treatment	n	Organic layer depth (cm)	Bulk density (g/cm^3)	Volumetric moisture content (cm^3/cm^3)	Manova test for overall treatment effect
CPCRW					
organic	6	4.8 ± 0.8 a	0.19 ± 0.14 a	15.6 ± 3.5 a	$F=8.07_{3,7}$
severe	6	1.0 ± 0.1 b	0.45 ± 0.04 a	28.1 ± 3.0 b	p=0.01
Delta					
organic	6	7.9 ± 0.9 a	0.15 ± 0.02 a	13.0 ± 3.7 a	$F=27.21_{3,8}$
severe†	6	2.2 ± 0.1 b	0.38 ± 0.01 b	25.9 ± 5.9 a	p=0.0002
mineral	6	0.0 ± 0.0 c	n/a	n/a	
Campbell Hwy.					
organic	9	4.3 ± 0.6 a	0.25 ± 0.05 a	10.4 ± 2.4 a	$F=14.68_{3,12}$
severe	9	0.7 ± 0.2 b	0.48 ± 0.04 b	27.2 ± 3.0 b	p=0.0003
Fox Lk. Experiment					
organic	6	6.6 ± 1.0 a	0.17 ± 0.03 a	16.0 ± 1.3 a	$F=15.24_{6,24}$
severe	6	1.1 ± 0.1 b	0.38 ± 0.06 a	25.6 ± 3.2 b	p<0.0001
mineral	6	0.0 ± 0.0 b	0.93 ± 0.09 b	32.4 ± 1.8 b	
Fox Lk. Natural					
organic	6	9.0 ± 1.1 a	0.13 ± 0.02 a	13.9 ± 2.0 a	$F=11.96_{6,24}$
severe	6	1.5 ± 1.1 b	0.47 ± 0.08 b	21.4 ± 1.8 a	p<0.0001
ash	6	0.0 ± 0.0 b	0.69 ± 0.05 c	15.1 ± 3.5 a	

† Organic layer depths in the severe plots at Delta generally include a 1-2 cm veneer of aolian-deposited silt above a layer of buried organics or charr.

Table 4.6: Results of statistical tests of severity and species effects on germination rates. Germination rates were standardized based on weight or number of viable seeds sown. Severity effects were tested in separate MANOVAs for each site (α=0.05), followed by orthogonal contrasts for sites with 3 treatment levels. Species and species*severity effects were tested in separate univariate ANOVAs (α=0.05/2=0.025). Data were rank-transformed prior to analysis.

Site	Severity effect	Variable	Species effect	Severity*species interaction
Campbell Highway	$F=34.99_{2,15}$ **p<0.0001**	seedlings/ g viable seed	F=4.14 **p=0.01**	F=5.77 **p=0.002**
		seedlings/100 seeds sown	F=5.81 **p=0.002**	F=3.12 ns
CPCRW	$F=6.53_{2,9}$ **p=0.017**	seedlings/ g viable seed	F=2.98 ns	F=0.42 ns
		seedlings/100 seeds sown	F=8.03 **p=0.0004**	F=0.02 ns
Fox Lake Experiment	$F=10.15_{4,30}$* **p<0.0001** *org vs. min+sev* $F=18.66_{2,14}$ p=0.0001 *min vs. sev* $F=5.56_{2,14}$ p=0.02	seedlings/ g viable seed	F=13.13 **p<0.0001**	F=8.20 **p<0.0001**
		seedlings/100 seeds sown	F=42.97 **p<0.0001**	F=3.46 **p=0.007**
Fox Lake Natural	$F=3.35_{4,30}$* **p=0.018** *org vs. ash+sev* $F=10.05_{2,14}$ p=0.002 *ash vs. sev* $F=0.80_{2,14}$ ns	seedlings/ g viable seed	F=7.50 **p=0.0004**	F=0.44 ns
		seedlings/100 seeds sown	F=21.44 **p<0.0001**	F=1.06 ns
Delta	$F=6.00_{4,30}$* **p=0.001** *org vs. min+sev* $F=12.88_{2,14}$ p=0.007 *min vs. sev* $F=10.73_{2,14}$ p=0.0015	seedlings/ g viable seed	F=4.24 **p=0.01**	F=1.76 ns
		seedlings/100 seeds sown	F=7.74 **p=0.0003**	F=2.13 ns

* F-statistic is Pillai's Trace.

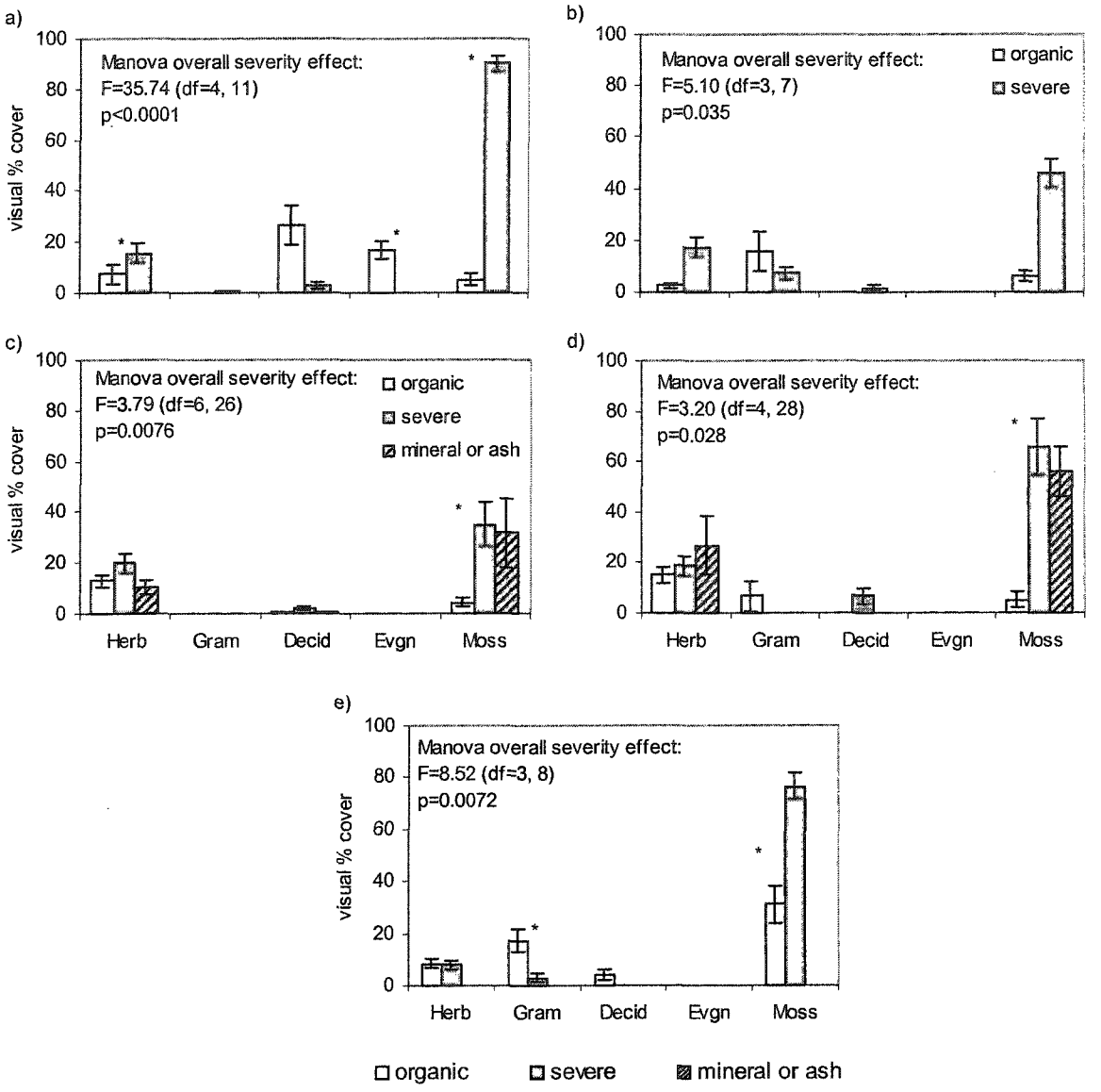

Figure 4.1: Cover of vegetation growth forms across severity treatments. Values are means (± 1 SE) of visual cover estimates across plots made in year three of the experiments. Results are shown separately for each site: a) Campbell Highway, b) CPCRW, c) Fox Lake Experimental, d) Fox Lake Natural, and e) Delta. Cover values of individual species were added to obtain growth form totals (herbs=Herb, graminoids=Gram, deciduous woody shrubs=Decid, evergreen woody shrubs=Evgn, and moss=Moss. Results of a MANOVA test for overall effects of burn severity on vegetation cover are summarized in each panel, and significant treatment differences for individual growth forms are indicated with an asterisk ($p<0.01$).

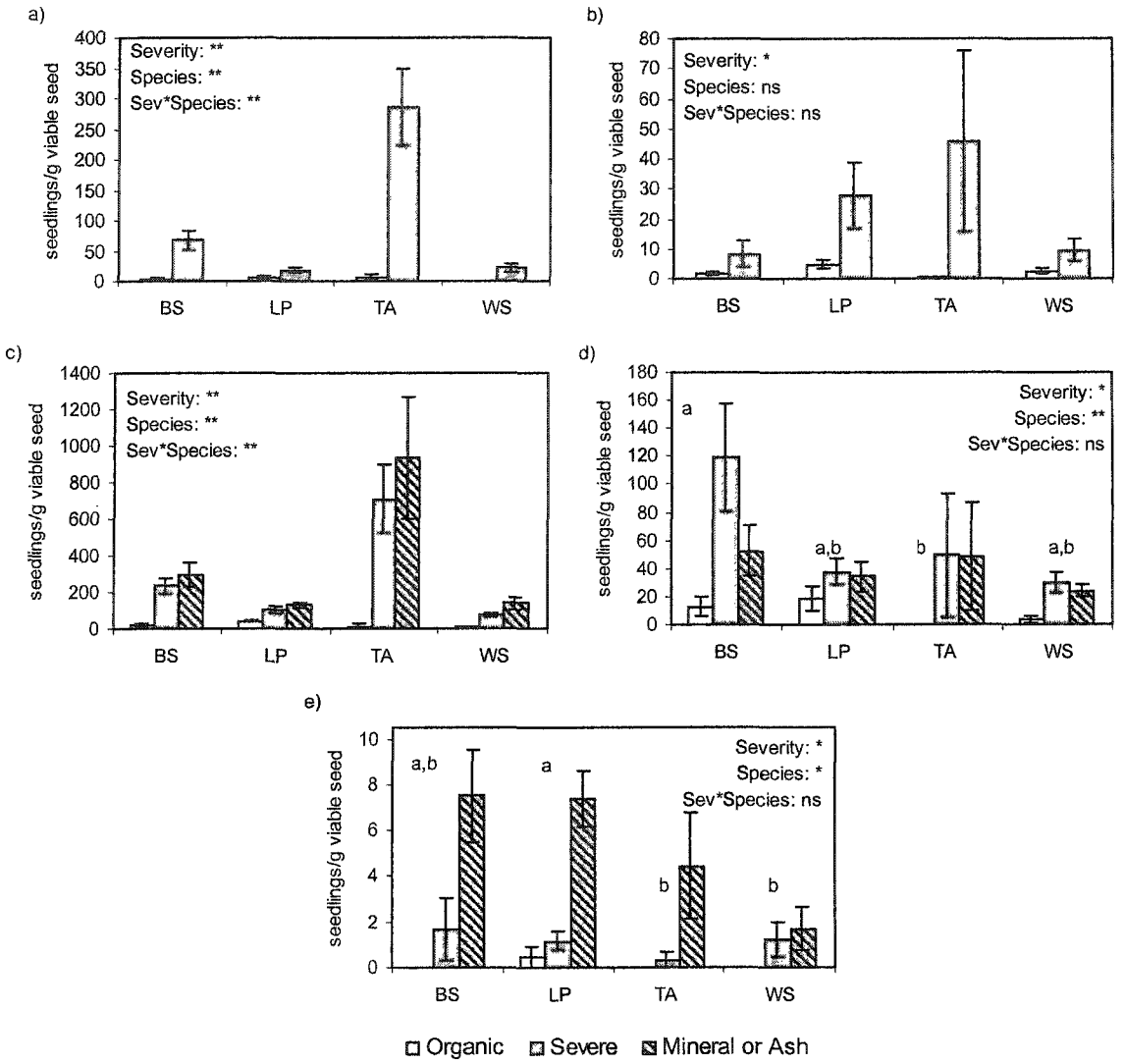

Figure 4.2: Seedling germination per gram of seeds sown, across sites and treatments. Graphs show the mean (± 1 SE) numbers of germinants per gram viable seed sown at individual sites: a) Campell Highway, b) CPCRW, c) Fox Lake Experimental, d) Fox Lake Natural, and e) Delta. Significance levels from F-tests of treatment effects are summarized within the panel (ns = not significant, * $p<0.025$, ** $p<0.001$). Burn severity effects were tested in a separate MANOVA (Table 4.4). Where there was no significante severity*species interaction, differences among species are indicated by different letters above the bars for each species (Tukey's multiple range test, $p<0.05$). All tests were performed on rank-transformed data.

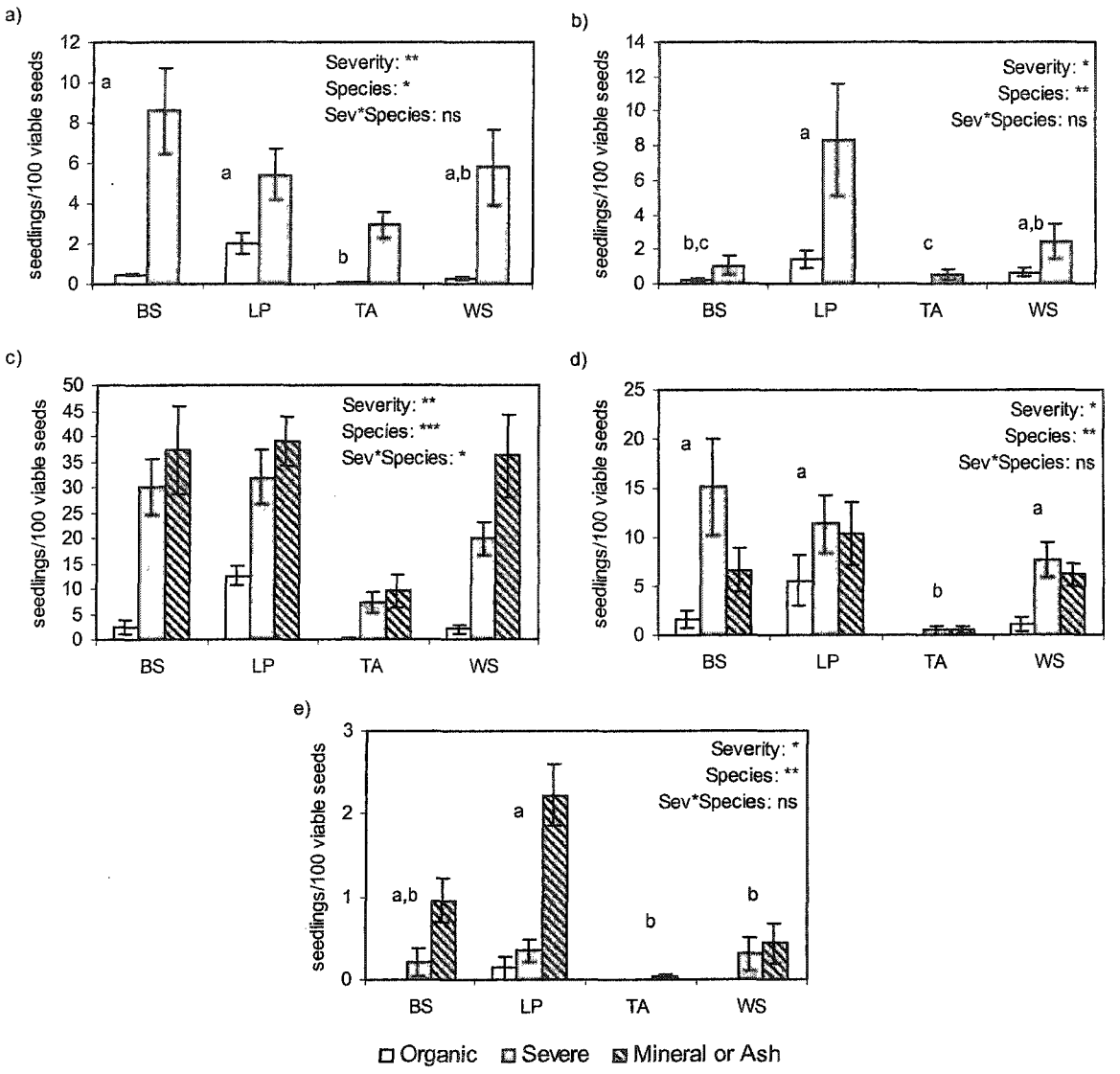

Figure 4.3: Seedling germination per number of seeds sown, across sites and treatments. Graphs show the mean (± 1 SE) number of germinants per 100 viable seeds sown at individual sites: a) Campell Highway, b) CPCRW, c) Fox Lake Experimental, d) Fox Lake Natural, and e) Delta. Significance levels from F-tests of treatment effects are summarized within the panel (ns = not significant, * $p<0.025$, ** $p<0.001$). Burn severity effects were tested in a separate MANOVA (Table 4.4). Where there was no significante severity*species interaction, differences among species are indicated by different letters above the bars for each species (Tukey's multiple range test, $p<0.05$). All tests were performed on rank-transformed data.

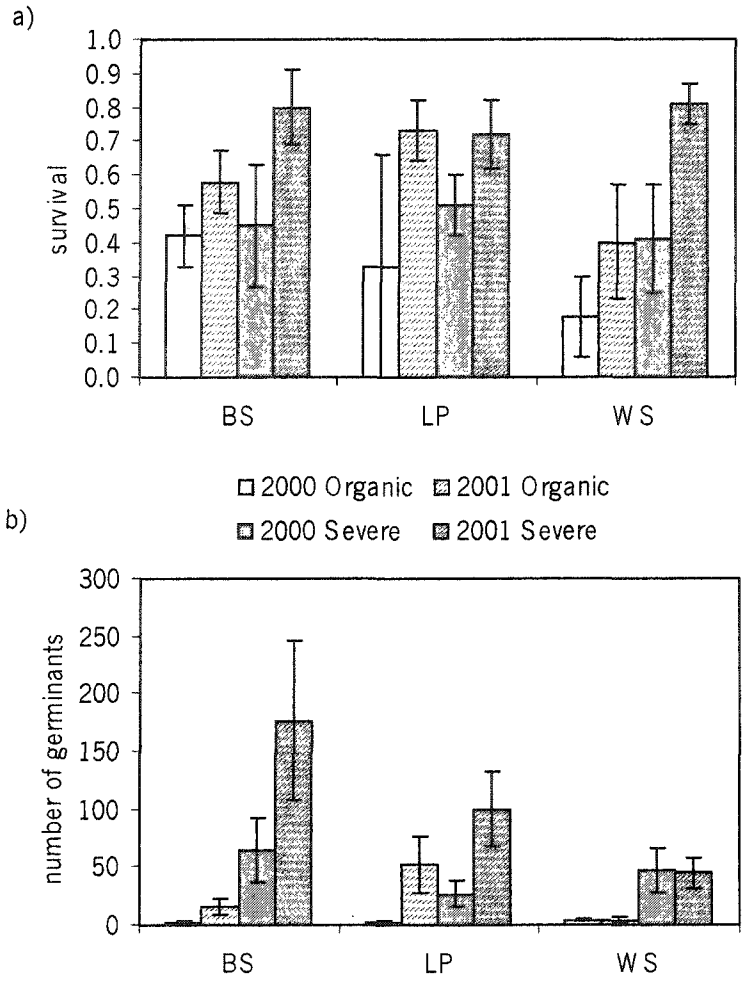

Figure 4.4: Survival of germinants across treatments and cohorts. Survival was estimated as the proportion of germinants surviving to the end of the experiment and averaged across study sites (graph (a), mean ± 1 SE, n=4), and the mean number of seedlings used in these estimates is shown in graph (b).

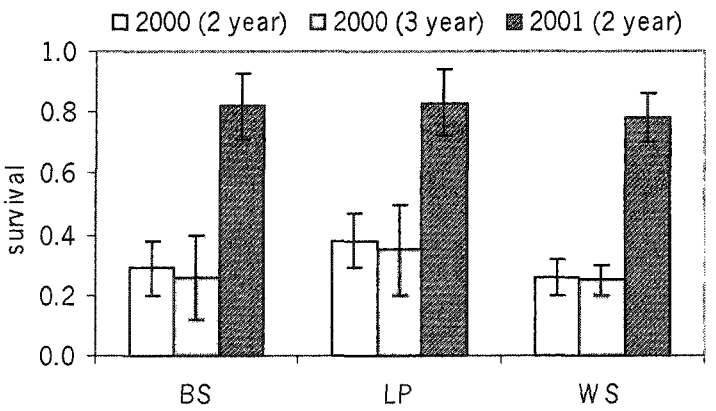

Figure 4.5: Seedling survival rates (mean ± 1 SE) in the severely-burned treatment at Fox Lake Experimental. Survival for the 2000 cohort is shown over a 2-year (white bars) or 3-year (grey bars) period following germination; survival of the 2001 cohort is shown over a 2-year period (hatched bars). Survival rates are calculated as the proportion of germinated seedlings alive at the end of the monitoring period (n=6).

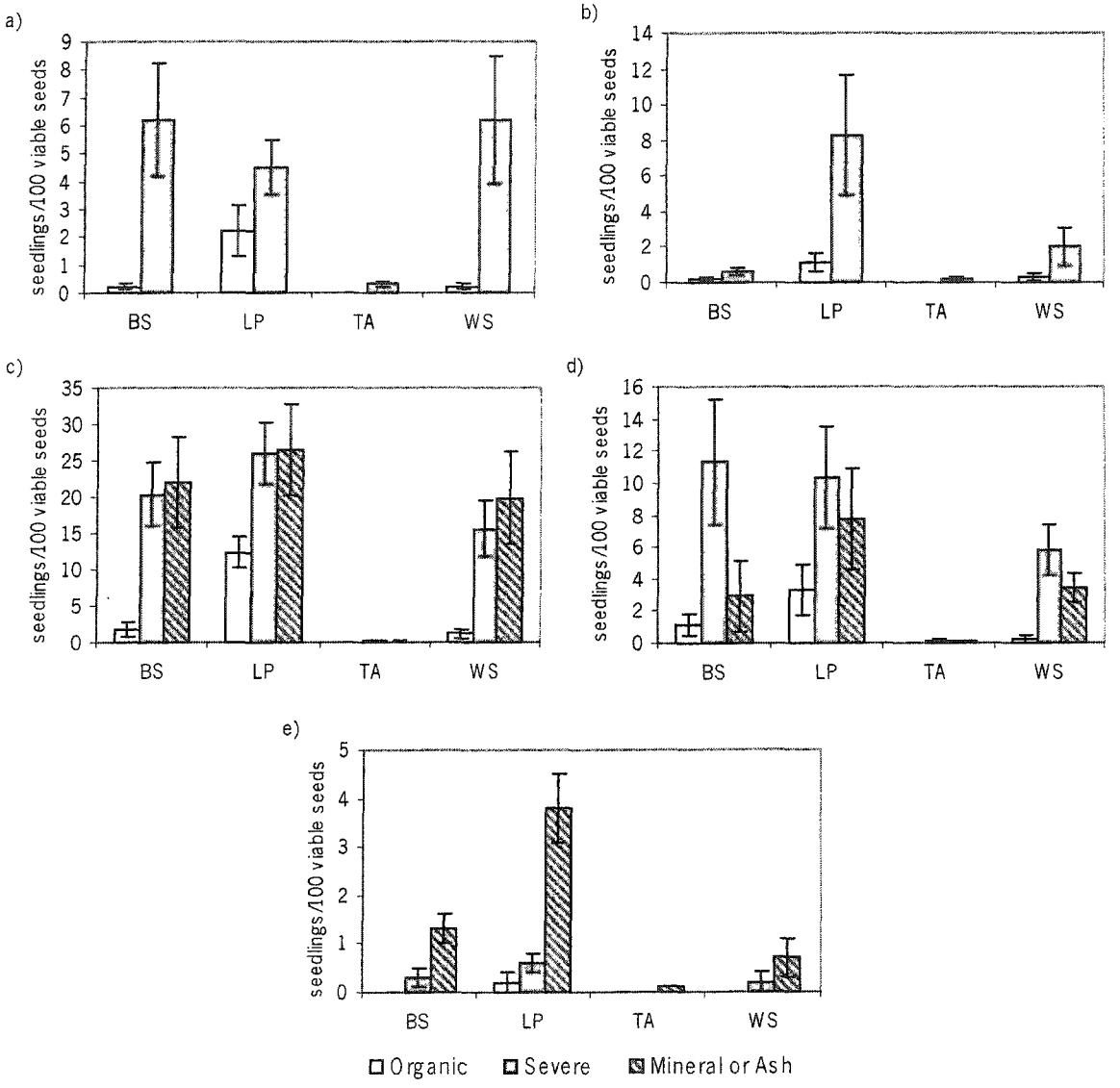

Figure 4.6: Net seedling establishment across sites and treatments. Each graph presents the mean (± 1 SE) number of established seedlings per 100 viable seeds sown at individual sites: a) Campell Highway, b) CPCRW, c) Fox Lake Experimental, d) Fox Lake Natural, and e) Delta. Established seedlings are those that were alive at the end of the experiment.

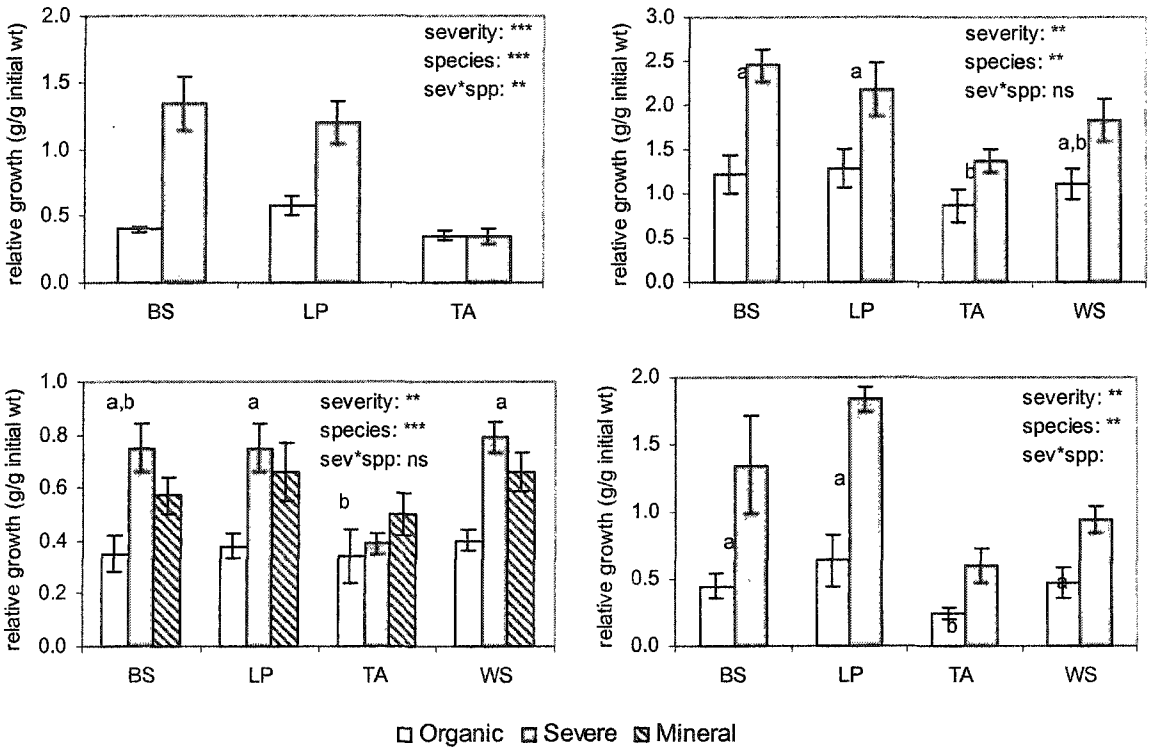

Figure 4.7: Growth response of transplanted seedlings to severity treatments. Individual panels represent different sites: a) Campbell Highway, b) CPCRW, c) Fox Lake Experimental, and d) Delta (note different y-axis scales). White spruce was not planted at the Campbell Highway site. For most treatment comparisons, n=6 or 9 (Table 4.1), except in the following cases: i) Fox Lake, aspen, organic treatment (n=5), and ii) Campbell Highway, aspen (n=7 and 5, in organic and severe treatments, respectively).

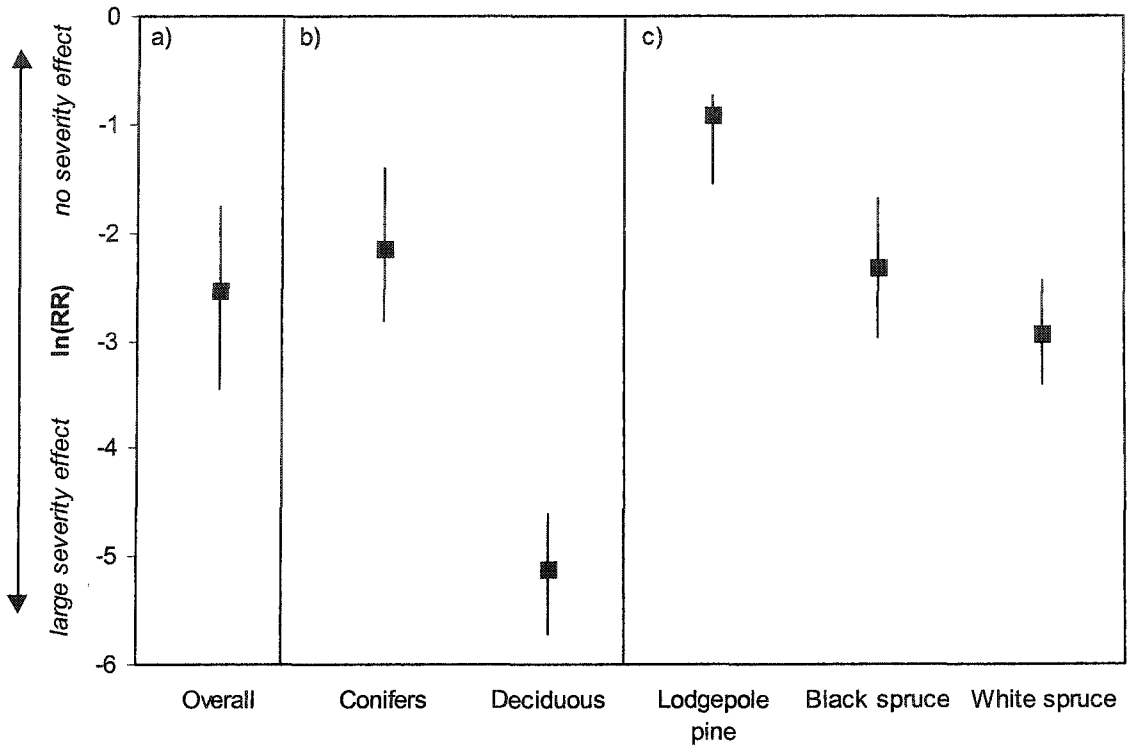

Figure 4.8: Results of a meta-analysis on experimental data from this study. Increasingly negative values indicate a proportionally larger difference between establishment on lightly-burned vs. severely-burned surfaces. Shown are the estimated effect sizes (ln(RR)) for each category, along with bootstrapped 95% confidence intervals. Each panel reflects a successive subdivision of categories, where a) shows the overall effect size across all species and experiments (n=16), b) compares conifers (n=12) and deciduous species (n=4), and c) compares lodgepole pine, black spruce, and white spruce (n=4 for each species).

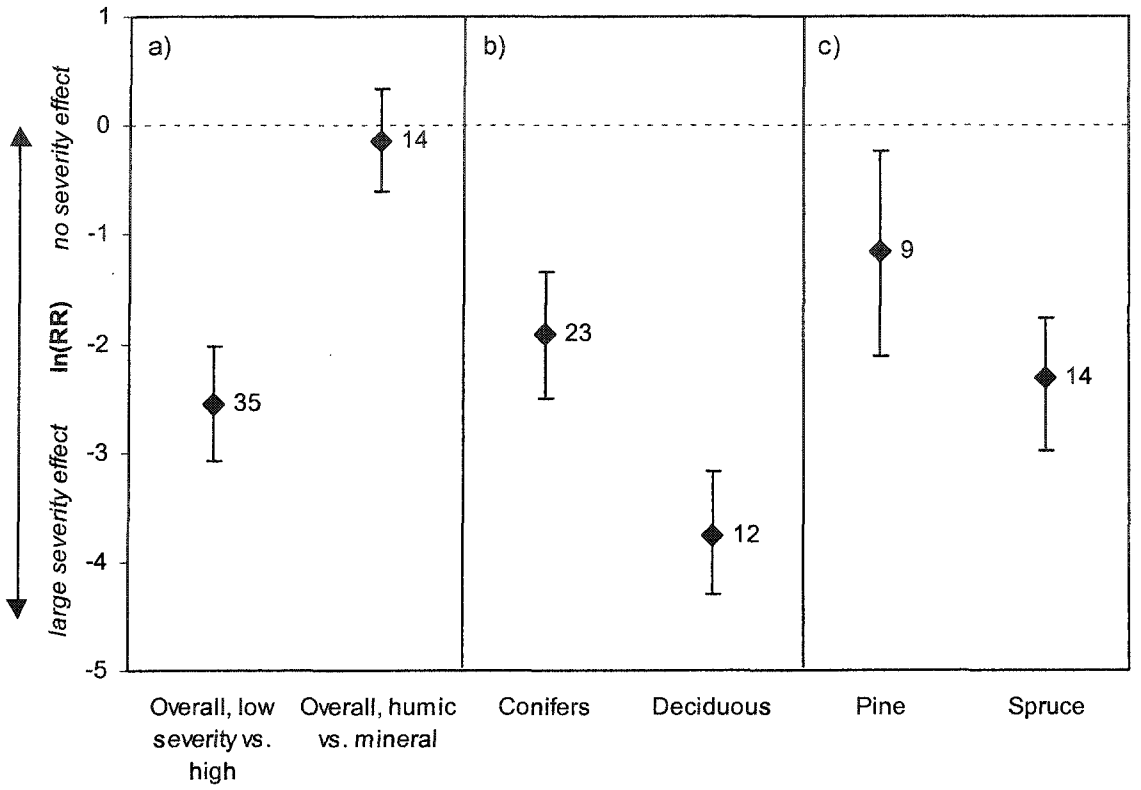

Figure 4.9: Estimated severity effect sizes from a cross-study meta-analysis of seedling establishment. Increasingly negative values indicate a proportionally larger difference between establishment on lightly-burned vs. severely-burned surfaces. Shown are the estimated effect sizes (ln(RR)) for each category, along with bootstrapped 95% confidence intervals. The number beside each mean is the sample size for that category. Panel a) shows the overall effect size across all species and experiments for comparisons of severely-burned vs. lightly-burned surfaces and for severe burns exposing mineral soil vs. humic soil. Panel b) compares the response of conifers and deciduous species to high and low severity and c) compares lodgepole pine, black spruce, and white spruce (high and low severity).

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CHAPTER 5: FIRE EFFECTS ON SUCCESSIONAL TRAJECTORY*

* Manuscript title: Fire effects on successional trajectory in the boreal forest of Northwestern Canada. Authors: J. F. Johnstone and F. S. Chapin, III. Unsubmitted manuscript.

Abstract

Although succession may follow multiple pathways in a given environment, the causes of such variation are often elusive. This paper describes how variations in fire interval mediate successional trajectory in conifer-dominated boreal forests of northwestern Canada. Tree densities were measured 5 and 19 years after fire in permanent plots and related to initial conditions of pre-fire vegetation, and site and fire characteristics. In stands that were >80 years of age when they burned, recruitment of conifers was significantly correlated with pre-fire species basal area, supporting the expectation of stand self-replacement as the most common successional pathway in these forests. In contrast, stands that were <30 years of age at the time of the previous fire had significantly reduced conifer recruitment and normal levels of deciduous recruitment. Deciduous recruitment was unrelated to pre-fire stand composition and appeared to result primarily from seed reproduction from off-site seed sources. Because early post-fire recruitment patterns have a strong effect on mature stand composition, young-burned stands are expected to persist as deciduous-dominated stands until they burn again. We suggest that climate-related increases in fire frequency could trigger more frequent shifts to deciduous-dominated successional trajectories that are difficult to reverse.

Introduction

An important shift in ecological thinking in recent decades has been the increased recognition of importance of non-linear relationships and threshold events in regulating ecosystem structure and functioning (Holling, 1986; Scheffer *et al.*, 2001; Gunderson and Holling, 2002). For example, several studies in aquatic and terrestrial systems have pointed to the importance of threshold responses to disturbance in controlling the emergence of alternate, self-perpetuating states of community composition and ecosystem functioning (Knowlton, 1992; Law and Morton, 1993; Scheffer *et al.*, 2001). Nevertheless, the processes that trigger threshold changes in ecosystems and the frequencies with which these events occur are poorly known.

In forest communities, it has been suggested that alternative patterns of succession may be initiated by threshold responses to changes in disturbance regime that are subsequently maintained by regeneration feedbacks, or 'neighborhood effects' (Frelich and Reich, 1999). Neighborhood effects involve positive or negative feedbacks to species re-establishment following disturbance. These interactions are capable of generating stable, predictable patterns of community composition across repeated disturbance cycles (Frelich and Reich, 1999). Such stable cycles can rapidly degenerate, however, when the disturbance regime is altered sufficiently to interrupt feedback processes of regeneration. When this occurs, a site becomes vulnerable to the establishment of new biota and rapid changes in community composition (Frelich and Reich, 1999; Camill and Clark, 2000; Franklin and Tolonen, 2000). If the new community type also has feedback effects that

favor its subsequent re-establishment, then return to the original community may be unlikely.

The climate of the boreal forest is currently warming as rapidly as any place on Earth (Keyser *et al.*, 2000; Serreze *et al.*, 2000) and is expected to lead to increases in fire frequency (Flannigan *et al.*, 1998). The two-fold increase in annual area burned in western North America in the last 20 years is probably linked to climate warming (Kasischke and Stocks, 2000). Could this large change in disturbance regime trigger shifts in successional trajectories that would influence the composition of boreal forest? This study addresses that question by documenting the consequences of natural variations in fire interval on succession trajectories in northwestern Canada.

In closed-canopy boreal forests, the most common successional trajectory is one that begins with the simultaneous establishment of deciduous and conifer trees after fire. Stands subsequently develop through a period of initial dominance by rapidly-growing, deciduous trees that succeeds over time to dominance of more slowly growing shade-tolerant conifers ('mixed-wood'; Van Cleve and Viereck, 1981; Bergeron, 2000). In general, post-fire patterns of establishment mimic patterns of pre-fire composition, with both conifers and deciduous species showing a high likelihood of re-establishment if they were present before the fire (Zasada *et al.*, 1992; Greene and Johnson, 1999). Deviations from mixed-wood succession may occur when either deciduous or conifer species fail to establish successfully after fire. Where deciduous species fail to establish, the length of time to development of a closed conifer canopy is shortened, but the characteristics of mature conifer stands are similar to those that followed a mixed-wood trajectory (Van

Cleve and Viereck, 1981; Bergeron, 2000). When conifer establishment is low, however, stand development leads in a different direction, with long-term maintenance of deciduous-dominated canopies (Cumming *et al.*, 2000). This deciduous trajectory represents a dramatic alternative to the mixed-wood or conifer-dominated trajectories, because ecosystem processes may be maintained in states characteristic of early succession, having high rates of litter production and decomposition, low rates of organic soil accumulation, open canopies, and relatively warm soils (Mann and Plug, 1999; Cumming *et al.*, 2000).

Deciduous-dominated trajectories are more common in the western boreal forests of North America (Rowe, 1972; Peterson and Peterson, 1992; Bergeron, 2000), where the fire frequency is higher (Payette, 1992), and shade-tolerant conifers are absent or relatively uncommon (Bergeron, 2000; Cumming *et al.*, 2000). Trembling aspen is often the dominant species of deciduous tree in these stands. Despite the short life-span of individual stems, aspen can maintain canopy dominance over long periods through asexual regneration in gaps (Cumming *et al.*, 2000). Gap dynamics may also occur in mixed-wood stands, but gaps that form in the deciduous canopy are likely to be filled by conifers where conifer seedlings or saplings are abundant (Bergeron, 2000). Differences between mixed-wood/conifer and deciduous pathways may be strengthened by feedbacks affecting the regeneration success of conifers versus aspen suckers. For example, in mature stands, the ability of aspen suckers to fill canopy gaps may be negatively affected by increases in humus depth (Lavertu *et al.*, 1994) or competition with sub-canopy conifers (Bergeron, 2000). On the other hand, conifer establishment may be reduced in

early post-fire stands by competition with rapidly-growing aspen suckers (Chapter 2), or in mature stands by poor seedling establishment on deciduous litter (Zasada *et al.*, 1992).

In this paper we use a long-term data set on post-fire vegetation succession to test how observed variations in fire regime (frequency and severity) affect the development of different successional trajectories in boreal forest. The availability of long-term monitoring records provides a unique opportunity to compare direct observations of initial post-fire site conditions with subsequent observations of vegetation regeneration. We focus our analysis on the regeneration patterns of four common tree species of the boreal forest, black spruce (*Picea mariana*), white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta* var. *latifolia*) and trembling aspen (*Populus tremuloides*), because of their importance in defining and contributing a large proportion of total biomass to different boreal community types. The resultant patterns are interpreted with respect to factors affecting the formation and maintenance of conifer/mixed-wood and deciduous-dominated succession trajectories in boreal forest.

Methods

Study area

The data for this study are collected from a series of permanent plots established in 1983 to monitor the long-term recovery of boreal forest vegetation after fire (Oswald and Brown, 1990). Plots were established in burn scars of three wildfires that occurred between mid-June and mid-August, 1982 along the Yukon/British Columbia border near

Watson Lake, Yukon Territory, Canada (60°N, 128°W). Two of the fires were lightning-initiated and reached sizes of 8,000 ha and 182,000 ha, and a third was human-caused and reached a size of 1,200 ha. Oswald and Brown (1990) provided detailed descriptions of the fires and pre-fire vegetation. Pre-fire vegetation was dominated primarily by black spruce and lodgepole pine, with occasional stands of white spruce, trembling aspen and paper birch (*Betula papyrifera*). Balsam poplar (*Populus balsamifera*) and western larch (*Larix laricina*) were minor components of the forests.

Field measurements

Forestry Canada established 39 permanent plots in 1983, one year after the fires occurred (Oswald and Brown, 1990). Road-accessible sample sites were selected to include a variety of soil types, topography, and pre-fire vegetation characteristics. Sampling in each burn was relative to the burn size, with 22, 11, and 6 plots in the largest to smallest burns. All sites were located at least 50m away from the original road right-of-way. Since 1983, three of the original plots were lost due to highway relocations. Each plot consisted of a 10x10 m sampling area, divided into four 5x5m subsections.

Physical and pre-fire stand conditions in each plot were measured in 1983 (Oswald and Brown, 1990). Physical measurements included slope angle, aspect, position on slope, and geomorphic landform type (Luttmerding *et al.*, 1990). Soil pits were dug in each plot, and soils were classified into a soil type based on the Canadian soil classification system (Agriculture Canada, 1987). The upper portion of the mineral soil was assigned to a soil texture class using the 'texture-by-feel' method (Luttmerding *et al.*,

1990). Site elevation was estimated from topographic maps. In order to characterize burn severity at each site, measurements were made of canopy burn severity class, proportion of exposed mineral soil, and mean residual organic layer depth. Canopy burn severity was ranked as being high where all aboveground woody stems <10cm diameter were consumed, moderate where all twigs <1 cm were consumed, and low where woody twigs and stems were scorched but not consumed.

Pre-fire forest composition was estimated one year after burning, based on species identification of partially-burned tree stems. Stands were characterized in terms of the dominant and sub-dominant tree species and total pre-fire stem density. In some plots, coarse woody material was completely consumed by the fire, and the dominant tree species were estimated from surrounding, more lightly burned stands or from pre-existing records (Oswald and Brown, 1990). In 2000-2001 we made more detailed estimates of pre-fire stand composition and structure by measuring the basal diameter of all canopy trees rooted in the plot when it burned. Species identifications were made based on bark, branch and cone morphology. We pooled individuals of black and white spruce because they consistently differ only in cone morphology, and we frequently found burned spruce individuals with no cones to indicate the species. Where we encountered conifer individuals of uncertain identity (at least one individual in 10 of 23 plots aged >80 yrs), we randomly assigned individuals to pine or spruce categories according to the proportion of identified individuals of each type in the plot. On average, 70 ± 4% (± 1 SE) of the pre-fire trees were conclusively identified in these plots.

Sites were categorized into different pre-fire age classes in 1983, but it is unclear in the original methods (Oswald and Brown, 1990) whether these ages were based on tree-ring counts or estimated from tree size. When the plots were re-surveyed in 2000-2001, we quality-checked the original age estimates by a) checking to make sure that the age class assigned to each stand was consistent with the size-distribution of the pre-fire stems, and b) counting rings on 1-4 basal tree disks in a subset of stands (n=10). We were limited in the number of stem discs we sampled because of time constraints and the high incidence of stem rot or beetle holes in the 20 year-old wood. Our estimates of minimum stand ages obtained from ring counts supported the original groupings of pre-fire age classes presented in Oswald and Brown (1990), and these groupings were used in subsequent analyses. In two cases (plots 22 and 24 in Oswald and Brown, 1990), however, fire scars indicated that the site had burned in the recent past, but not all trees had been killed. These stands were originally classed in the mature age category, but were switched to the younger age category in this analysis.

Repeated measurements of tree species density were made in the plots during the first decade after fire (Oswald and Brown, 1990). In this study, we use seedling count data from 1987, 5 years after fire (Oswald and Brown, 1990), to represent initial post-fire tree recruitment, and more recent stem counts to represent established stand composition. Recent counts were made in 16 plots in July 2000 and 20 plots in June 2001, which we collectively refer to as year 19 post-fire. Observations of tree stem counts were made in 5x5m subsections of the main plot, and then summed to obtain a whole-plot estimate. All tree seedlings were identified to species, except for black and white spruce, which could

not be confidently distinguished in the case of small seedlings. These species were pooled in our analysis, but we estimate that black spruce was the most common spruce type. Approximately 75% of the seedlings we examined had red hairs present on the one year-old twigs, a criterion that can be used to identify black spruce individuals (Cody, 1996). An unknown portion of the remaining seedlings may have also been black spruce individuals that were too small to have produced twigs with hairs.

Statistical analysis

We examined all continuous data for departures from normality and heteroscedasticity. We corrected for skew in the stem count and basal area data with natural log and square root transformations, respectively. We identified 2 of the 36 plots in our sample that were consistent outliers in our analyses. One of these plots (plot 27) represented the only mature aspen stand sampled in the study. We removed this plot from the dataset, and consequently emphasize that our results refer primarily to conifer-dominated or mixed conifer/deciduous stands. The second outlier stand (plot 25) had a large pre-fire basal area of lodgepole pine, but was unusual in having no established pines when measured 19 years after fire. Observations made 5 years after fire indicated pine seedling densities of 0.39 seedlings/m^2 (Forestry Canada, unpublished data), but in years 10 and 19, no pine seedlings were observed in the plot. Evidence of extensive hare herbivory was, however, noted in year 10, suggesting that the absence of pine seedlings may have been due to herbivore effects. Aspen stems in the plot did not show a decline in density, but average stem heights in year 10 were the lowest recorded in any of the plots, a pattern that also suggests intense herbivore browsing. Because this plot appeared to be

an isolated case in which herbivore effects strongly modified stand composition patterns, we did not include it in the analysis of the 19-year post-fire dataset.

We used estimates of pre-fire stand ages as a surrogate indicator of the length of the previous fire-return interval. All of the stands fell into one of two classes, young-burned stands that were less than 30 years old, and mature-burned stands that aged between 80 and 130 years. Young-burned stands were uniformly located on Brunisol-type soils, while mature-burned stands occurred on a mixture of Brunisols, Regosols and Gleysols. Because differences in general soil type are likely to represent substantial differences in physical site or vegetation factors (Agriculture Canada, 1987), we excluded sites that were located on Regosols (n=2) and Gleysols (n=4) from our analysis of fire interval effects. This resulted in a final sample size of 13 young-burned stands and 16 mature-burned stands.

We performed our data analysis using SAS v. 8.02 (SAS Institute, Cary, N.C.). We tested for significant differences in tree regeneration patterns between the two age classes using multivariate analysis of variance (MANOVA) of post-fire densities of spruce, pine, and aspen, followed by separate ANOVA tests on each species (SAS Proc GLM). We also tested for significant differences in environmental conditions between the two age classes using a MANOVA of slope angle, slope aspect, elevation, soil drainage and soil texture. Soil drainage data consisted of four classes ranging from very rapid to moderate drainage, and soil texture consisted of six classes ranging in coarseness from sand to silt loam. We translated slope aspect data into ordinal scale by giving north-facing slopes a value of -1, south-facing slopes a value of $+1$, and level, east- or west-

facing slopes a value of 0. Intermediate aspects were given intermediate values (*i.e.*, NE=-0.5). We were unable to derive an ordinal ranking for geomorphic terrain origin, and did not include this factor in the analysis. Other measured environmental variables, such as slope position, showed little variation among sites and were excluded from the analysis.

We tested whether observed differences in post-fire tree density were due to direct effects of fire interval length, or to indirect effects of co-varying environmental factors by conducting a set of partial correlation and multiple regression analyses. We used principle components analysis (PCA; SAS Proc Princomp) to decompose inter-correlated environmental variables into orthogonal eigenvectors that were then used as variables in the analyses. We first used simple correlation coefficients to identify the environmental variables that were most strongly related to stand age at burning. We then calculated partial correlation coefficients between stand age class and post-fire species stem density while controlling for the effects of the age-correlated environmental variables. In order to address the possibility that multiple, weakly-correlated environmental variables may account for the observed age effects, we used multiple linear regression (SAS Proc Reg) to construct and compare two alternative model types, one that included age as a variable in the model, and one that included only environmental effects. For each species, we selected the best model of each type as that having the lowest corrected Akaike Information Criteria (AIC_c) value (Anderson *et al.*, 2000). We then compared the best models of each type with each other on the basis of AIC_c, C(p), and R^2 statistics to

determine whether the inclusion of age substantially improved the fit or predictive ability of the model.

Significant correlations between pre-fire species basal area and post-fire stem densities in year 19 were tested using nonparametric correlation (Spearman's *r*; Conover, 1999), because of heteroskedastic residuals using either the raw or transformed data. This analysis was performed for mature-burned stands located on all soil types (n=21). We also tested for effects of burn severity on stand regeneration patterns in mature-burning stands. Because of high levels of multi-collinearity between burn severity, environmental, and pre-fire stand composition, we were unable to test for direct effects of burn severity on regeneration. Instead, we tested whether knowledge of burn severity improved our ability to predict species regeneration patterns from environmental and pre-fire stand data. Prior to the analysis, we used PCA to generate orthogonal burn severity variables that described variation in crown severity, mineral soil exposure, and residual organic layer depth. We then compared the best models to predict year 19 species regeneration density in two classes of model, one with burn severity effects, and one without. Model selection was carried out as described above for the stand age models.

Results

The length of the previous fire return interval had a strong impact on post-fire regeneration patterns (Figure 5.1). Stands that burned at a young age had lower seedling establishment in the years immediately following the fire (MANOVA on 5-year seedling density, $F=11.74$, $df=3/24$, $p<0.0001$). This effect was maintained by the established

vegetation and, 19 years after fire, tree densities were significantly lower in stands that burned at a young age compared to mature-burned stands (MANOVA $F=15.54$, $df=3/24$, $p<0.0001$). The effects of fire return interval length on regeneration density differed among species. Spruce and pine both showed substantially lower post-fire stem densities in the young-burned stands than in stands that were mature when they burned (ANOVA $F=45.08$ and 13.96, $p<0.0001$ and 0.0009 for spruce and pine, respectively, at 19 years). In contrast, aspen stem densities were unaffected by stand age at burning (ANOVA $F=0.08$, $p=0.77$). This difference in species response to length of fire interval resulted in a higher proportion of deciduous-dominated or mixed deciduous/conifer stands regenerating on young-burned sites compared to mature-burned sites (Figure 5.2b and 5.2c). In contrast, patterns of pre-fire dominance were relatively similar between the two age classes, with most stands being dominated by pine or a mixture of pine and spruce (Figure 5.2a).

Because the variations in fire-return interval observed in this study are the result of natural events, rather than experimental manipulation, length of fire interval might be confounded with the effects of co-varying environmental factors. The multivariate analysis of variance on environmental variables of slope, aspect, elevation, soil texture and soil drainage indicated a significant difference in overall environmental conditions between stands that burned when they were young vs mature ($F=4.11$, $df=5/22$, $p=0.009$). This difference was largely due to a higher frequency of sites with well-drained soils in the young-burned relative to the mature-burned class (ANOVA $F=6.80$, $p=0.015$; Figure 5.3). Otherwise, our analysis detected no significant differences in aspect, slope,

elevation, or soil texture with respect to pre-fire age (univariate ANOVA's, $p>0.1$). However, soil texture and elevation were both significantly correlated with soil drainage ($r=0.44$ and 0.50, $p=0.02$ and 0.006, respectively), indicating the potential for complex relationships between fire-return interval and environmental gradients. Variation associated with soil drainage, soil texture, and elevation was decomposed into orthogonal eigenvectors using PCA, with the first and second eigenvectors accounting for 64 and 19 percent of the variation in the dataset. Correlation analysis found only the second environmental eigenvector to be significantly correlated with stand age at burning ($r=-0.52$, $p=0.005$), indicating that young-burned stands were more likely to occur on coarse-textured, high elevation sites, i.e., sites likely to have dryer soils. When these stand age-related environmental effects were statistically controlled for in a partial correlation analysis, both spruce and pine continued to show a significant response to fire interval (partial $r=0.79$ and 0.47, $p<0.0001$ and 0.01 for spruce and pine, respectively, $n=28$). Aspen density remained uncorrelated with stand age at burning (partial $r=0.06$, $p=0.74$, $n=29$). In a similar fashion, multiple regression analysis indicated that the inclusion of stand age at burning as a factor in the models increased the proportion of explained variation and improved the fit of models for spruce and pine, but not aspen (Table 5.1).

In mature-burned stands, tree stem densities of spruce and pine measured 19 years after fire were significantly related to pre-fire species basal area (Spearman $r=0.48$ and 0.55, $p=0.03$ and 0.01, respectively; Figure 5.4). Aspen regeneration density was not correlated with pre-fire aspen basal area or with aspen presence or absence in the pre-fire stand ($p>0.1$). Only 5 of 21 mature-burning stands in this analysis had aspen present in

the sample plot prior to the fire; two additional sites had pre-fire aspen within 10 m of the plot borders. Post-fire aspen (seedlings or resprouts), in contrast, was found in all of the sampled plots.

Variation in burn severity within mature-burned stands was intercorrelated with several environmental factors, making the estimation of direct effects difficult. Instead, we used regression model comparisons to test whether knowledge of burn severity improved our ability to predict species regeneration patterns. On average for the three species, knowledge of burn severity increased the amount of variance explained by about 10% (Table 5.2). Standardized regression coefficients indicated that regeneration of spruce and aspen were positively and negatively, respectively, related to residual organic layer depth, and pine was positively related to crown fire severity and mineral soil exposure.

Discussion

Our results show a large difference in regeneration patterns between stands that burned at a young versus mature age. Average fire return intervals in boreal spruce and pine forests of western North America are frequently estimated in the range of 50-150 years (Yarie, 1981; Johnson and Larsen, 1991; Payette, 1992; Larsen, 1997). Thus, the fire-free periods experienced by the mature-burned stands in this study (80-150 yrs) appear to represent normal fire frequencies for the region. In contrast, fire return intervals of less than 30 years, as experienced by our young-burned stands, are likely to be unusual disturbance events under the historical fire regime. Historic fires recorded in the Yukon

Fire History database indicate that approximately 6% of the area burned in the decades of 1980 and 1990 (0.062/1.1 and 0.11/1.8 million ha, respectively) overlapped with fire scars in the three preceding decades (personal communication, D. Milne, Fire Management Branch, Indian and Northern Affairs Canada). Spruce and pine both exhibited a significant reduction in post-fire regeneration in response to a short fire-return interval, with spruce showing a larger and more consistent reduction than pine. These responses were significant even when the effects of co-varying environmental factors were included, suggesting that low recruitment densities were a direct effect of the reduction in fire return interval. In contrast to the conifers, aspen regeneration rates were insensitive to variations in fire return interval.

The species-specific responses to fire interval length can be explained by differences in life history strategies between spruce, pine and aspen. The decline in conifer recruitment associated with a short fire interval appears to be a consequence of two life history attributes of these species: a) a strong dependence on local seed rain for recruitment, and b) low seed production rates among young trees. At least 75% of the spruce seedlings counted in this study were estimated to be black spruce. Both black spruce and lodgepole pine store seeds in serotinous cones in the tree canopy, which open up after heating by fire (Zasada *et al.*, 1992). Canopy storage of seeds is a strategy that increases local seed availability after disturbance while decreasing contributions of seed to annual, longer-distance dispersal. The dependence of black spruce and lodgepole pine on local seed rain for regeneration is supported by the positive correlations between

regeneration density and pre-fire basal area observed in this study and elsewhere (Greene and Johnson, 1999).

Given the importance of local seed rain to conifer regeneration, factors that affect seed availability are also likely to influence regeneration success. Both pine and spruce do not start producing viable seed until two or three decades after establishment, and cone serotiny rates are generally low among juveniles (Burns and Honkala, 1990; Zasada *et al.*, 1992). Because both production and storage rates of seed are low for young trees, stands that burn at a young age are likely to have very low potential for post-fire conifer recruitment. This period of low recruitment potential may be shorter for lodgepole pine than black spruce, because of pine's capacity to produce cones at an earlier age (Lotan and Perry, 1983; Bonnor, 1989; Burns and Honkala, 1990). In our plots, for example, we observed occasional cones on pine saplings 19 years after fire, but no cones on spruce saplings. In addition, not only are young trees likely to produce low amounts of seed, but their small stature also makes then more likely to experience complete crown combustion in a fire, destroying any seed reserves that were produced.

In contrast to the conifers, deciduous species such as trembling aspen, balsam poplar and paper birch have regeneration strategies that capitalize on asexual re-sprouting from roots or stumps, or long-distance transport of small, wind-blown seeds (Zasada *et al.*, 1992). Asexual regeneration in aspen individuals can occur after only 1 year of growth (Zasada *et al.*, 1992), indicating that there would be little effect of a shortened fire return interval on re-sprout capacity. Likewise, sexual regeneration from off-site seed would not be directly affected by stand age. In this study, there was no relationship

between aspen regeneration density and pre-fire aspen basal area or abundance. Because we observed substantial aspen regeneration at sites where there were no pre-fire aspen stems in the plot or surrounding locality, we hypothesize that seed regeneration played a large role in aspen recruitment at our sites. Although this form of regeneration is generally considered uncommon (Peterson and Peterson, 1992), it does occur (Kasischke *et al.*, 2000). Whether aspen recruitment occurs by seed or sprouting, fire interval effects would be expected to minimal because of the lack of local age-dependence in the reproductive processes.

Patterns of burn severity may also play a role in driving species regeneration patterns. In this study, knowledge of burn severity improved our ability to predict regeneration patterns of all three species. The direction of burn severity effects on pine and aspen are consistent with experimental studies that show a positive effect of increased mineral soil exposure, and a negative effect of increased residual organic layer depth on seedling establishment rates (Zasada *et al.*, 1983; Herr and Duchesne, 1995; Charron and Greene, 2002). The positive relationship between residual organic layer depth and spruce regeneration most likely reflects the tendency of black spruce to dominate moist, organic-rich soils (Burns and Honkala, 1990). This interpretation highlights the fact that, in the absence of experimentation, we cannot determine the causative processes connecting fire variations with regeneration patterns. Although this is also true of our analysis of fire interval effects, we feel that the data in this study point strongly to a biologically-plausible, causative pathway between fire interval and species regeneration capacity.

This study has focused on describing the effects of variations in fire regime on patterns of post-fire regeneration and early stand development. Although the time span of study is short relative to the time scales of succession, an emphasis on early regeneration is justified because of the strong links between early regeneration patterns and mature stand composition. In the boreal forest, stand reconstructions have repeatedly demonstrated that in the majority of cases, it is the seedlings that establish within the first decade after fire that dominate the canopies of mature stands (Johnson and Fryer, 1989; Lavoie and Sirois, 1998; Gutsell and Johnson, 2002). In our study, we found that conifer seedling establishment 5 years after fire was greatly reduced in stands that burned after a short fire interval, and these effects persisted 19 years after fire. Demographic analyses of this and other long-term datasets have shown that net seedling recruitment is generally complete by 10 years after fire, and that patterns of tree composition observed in 20-30 years after fire largely reflect the composition patterns established within 3-5 years after fire (Chapter 2).

Once the initial phase of establishment is over, the pathway of succession has been largely set, and there appears to be substantial inertia in following a given pathway until a stand is disturbed by fire or some other agent (Figure 5.5). In stands with successful conifer regeneration, conifers usually dominate at maturity, even if deciduous species also establish successfully. Deciduous species compete poorly in the canopy with conifers because of their shorter life spans and lesser shade tolerance (Van Cleve and Viereck, 1981; Bergeron, 2000; Gutsell and Johnson, 2002). If conifers establish poorly, however, deciduous species are able to maintain stand dominance across fire-free

intervals through asexual regeneration in forest gaps (Cumming *et al.*, 2000). Conifer invasion of mature deciduous stands is hindered by both low seed availability (Stewart *et al.*, 1998; Greene and Johnson, 2000) and poor seedling establishment on forest litter or moss (Simard *et al.*, 1998; Purdy *et al.*, 2002). In addition, in areas with frequent fire, those conifers that do manage to establish in the deciduous understory are unlikely to obtain dominance before the stand burns again (Mann and Plug, 1999). Once a stand does burn, patterns of regeneration after fire frequently result in stand self-replacement, because of reproductive feedbacks that favor the re-establishment of the pre-existing vegetation. These feedbacks include direct effects on the availability of seed or resprouts (Greene and Johnson, 1999), as well as indirect effects mediated by incomplete combustion of thick organic layers (Chapter 4; Zasada *et al.*, 1983) or competition among regenerating sprouts and seedlings (Chapter 3).

In conclusion, this study demonstrates that a short fire return interval can lead to a failure of post-fire conifer recruitment, causing the initiation of an alternative, deciduous-dominated community. Once initiated, these communities are likely to be stable over time because of positive feedbacks to species maintenance and regeneration (Figure 5.5). The patterns observed in this study support other modeling and field studies indicating that variations in fire frequency may shape landscape patterns of deciduous or conifer dominance (Suffling, 1995; Mann and Plug, 1999). Our data illustrate that changes in fire interval may 'short-circuit' species regeneration pathways, and lead to a rapid and dramatic shift in successional trajectory. This study supports the hypotheses that systems with strong neighborhood effects may show a pronounced and sudden regime shift in

response to changes in disturbance regime, and that once a regime shift has been initiated, it may be stabilized by the same reproductive feedbacks that reinforced the previous regime (Frelich and Reich, 1999). In the western boreal forest, if fire frequency changes in response to climate warming (Flannigan *et al.*, 1998), unusual fire events that interrupt reproductive pathways may play a key role in shaping landscape responses by mediating shifts between alternative deciduous- and coniferous-dominated community states. Because deciduous and conifer communities differ in many attributes of ecosystem function, such as land-atmosphere energy exchange (Chapin *et al.*, 2000) and carbon turnover (Hobbie *et al.*, 2000), changes in the relative dominance of these community types may have important impacts on long-term ecosystem response to climate change.

Table 5.1: Summary of regression models to predict post-fire regeneration density. Models were developed separately for spruce, pine, and aspen (n=29). For each species, the models were split into those including and excluding age as a predictor variable, and the 'best' model of each type was selected based on the lowest AIC_c score. Variables env1, env2, and env3 are PCA eigenvectors that represent negative (env1) and positive (env2, env3) moisture gradients derived from correlated effects of soil drainage, soil texture, and site elevation. A plus or negative sign beside a model variable indicates the direction of effect on regeneration density. For each species, the better of the two models was selected to minimize the C(p) and AIC_c statistics, and is shown in bold font.

Predicand	Model type	Variables in best model	R^2	C(p)-p†	AIC_c
ln(spruce density)	**with age**	**age (+)**	**0.57**	**0.52**	**11.6**
	without age	slope (+)	0.08	26.26	33.6
ln(pine density)	**with age**	**age (+)** **env3 (+)**	**0.49**	**1.55**	**21.58**
	without age	env1 (+) env2 (-)	0.37	9.51	27.48
ln(aspen density)	with age	age (+) env1 (-)	0.28	0.94	3.28
	without age	**env1 (-)** **aspect (-)**	**0.33**	**0.94**	**1.24**

† Values of C(p) are given as absolute deviations from the expected value of p, the number of variables in the model.

Table 5.2: Summary of regression models to predict post-fire regeneration density for mature-burned stands. Models were developed separately for spruce, pine, and aspen (n=29). For each species, the models were split into those including and excluding age as a predictor variable, and the 'best' model of each type was selected based on the lowest AICc score. Variables 'fire1' and 'fire2' are PCA eigenvectors that represent burn severity effects. Fire1 is positively correlated with crown severity class and % mineral soil exposure, and fire2 with depth of the residual organic layer. A plus or negative sign beside a model variable indicates the direction of effect on regeneration density. For each species, the better of the two models was selected to minimize the C(p) and AIC_c statistics, and is shown in bold font.

Predicand	Model type	Variables in best model	R^2	C(p)-p†	AIC_c
ln(spruce density)	**with severity**	**fire2 (+) elevation**	**0.45**	**0.45**	**-3.47**
	without severity	rt(spruce basal area) (+) elevation	0.39	2.30	-1.36
ln(pine density)	**with severity**	**fire1 (+) rt(pine basal area) (+) elevation**	**0.52**	**1.01**	**14.21**
	without severity	rt(pine basal area) (+) elevation	0.40	1.55	15.94
ln(aspen density)	**with severity**	**fire2 (+) elevation**	**0.52**	**1.01**	**-6.26**
	without severity	elevation	0.37	2.61	-3.38

† Values of C(p) are given as absolute deviations from the expected value of p, the number of variables in the model.

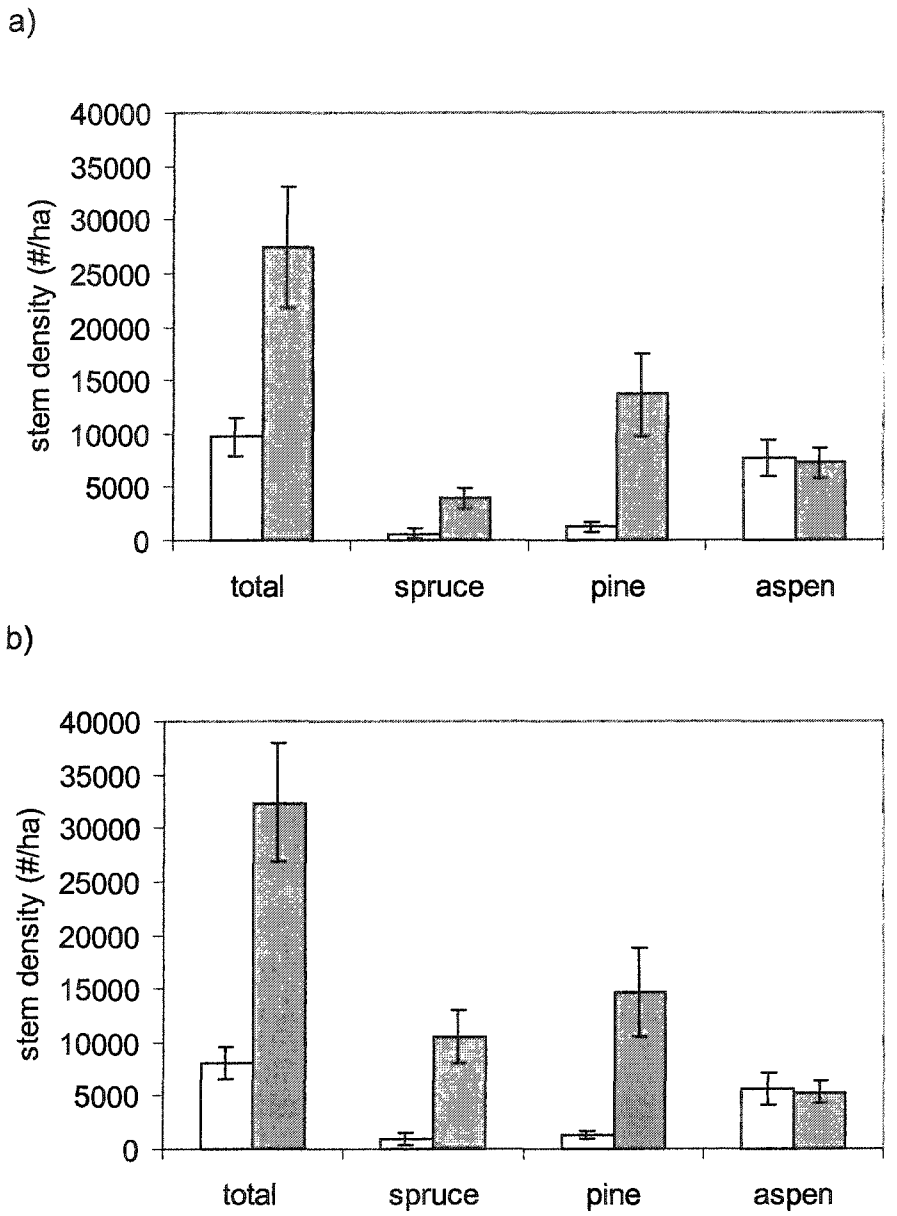

Figure 5.1: Mean (± 1 SE) tree stem density in regenerating stands. Stem densities were measured (a) 5 years and (b) 19 years after fire, in stands that burned at ages of less than 30 years (light bars, n=13) or ages of 80-130 years (dark bars, n=17). Density is shown as total tree stems, and divided into spruce (black and white), lodgepole pine, and trembling aspen.

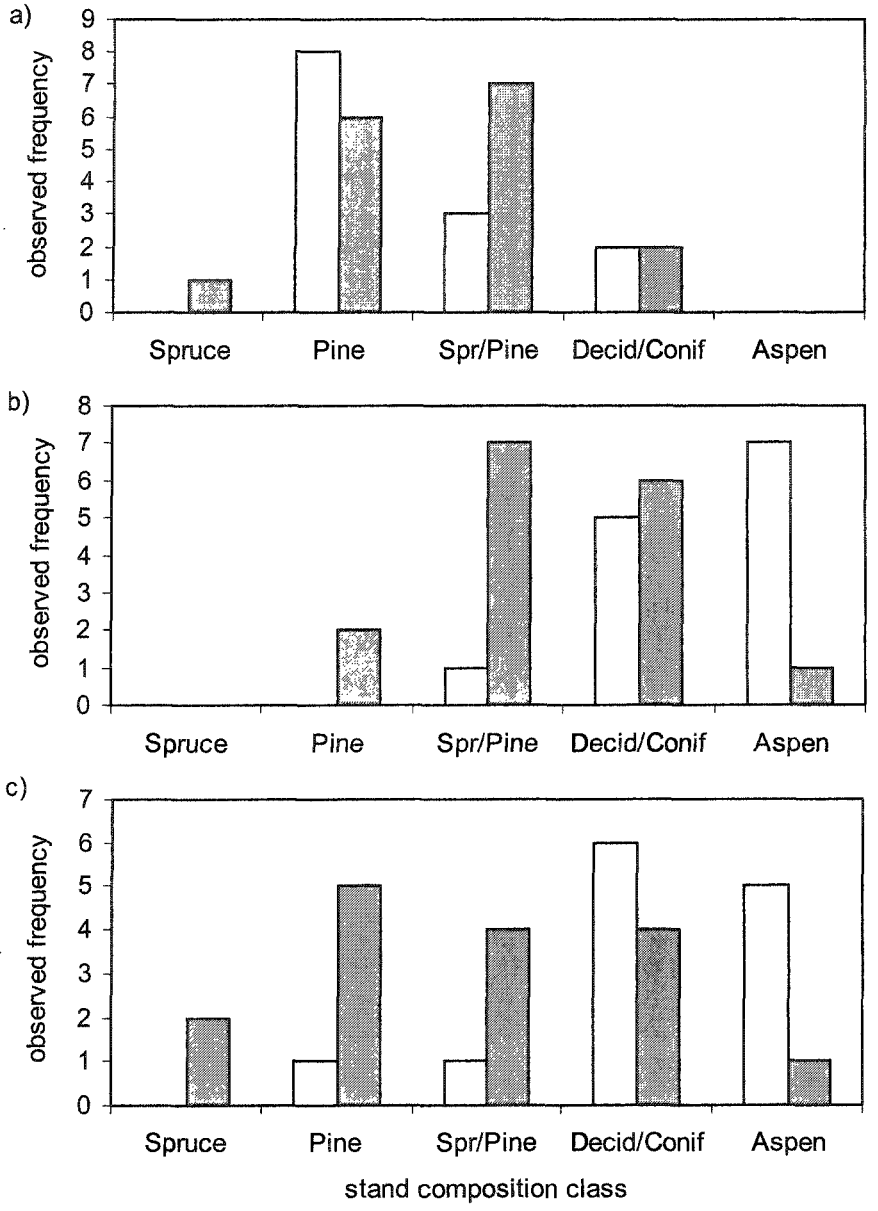

Figure 5.2: Frequency of stand dominance classes in (a) pre-fire and (b-c) post-fire stands. Frequencies are shown separately for stands that burned at ages of less than 30 years (light bars, n=13) or ages of 80-130 years (dark bars, n=17). Pre-fire stand dominance classes are based on qualitative estimates made one year after burning (Oswald and Brown, 1990). Post-fire stand dominance is calculated from stem counts made (a) 5 years and (b) 19-years post-fire. Stands dominated by a single species have one species comprising >50% and all other individual species comprising <25% of the stems, and stands with mixed-species dominance have more than one component species with over 25% of the stems.

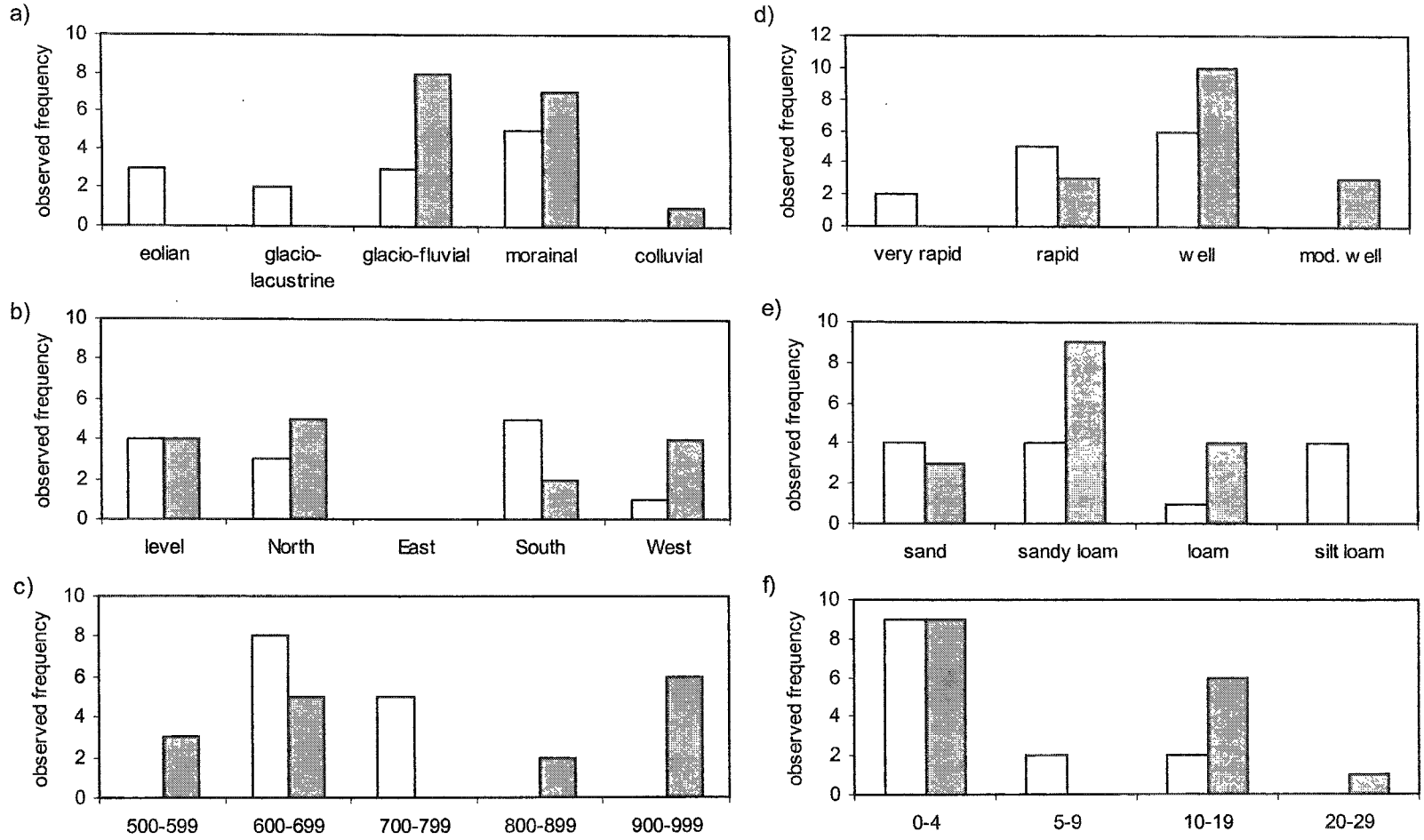

Figure 5.3: Frequency histograms showing the distribution of stands relative to environmental factors. Distributions are shown separately for young (light bars, n=13) and mature (dark bars, n=23) burn classes across different environmental site factors: a) origin of surficial material (ordered from highly sorted to unsorted), b) site aspect, c) site elevation in meters, d) drainage class, e) soil texture (ordered from coarse to fine), and f) slope angle in degrees.

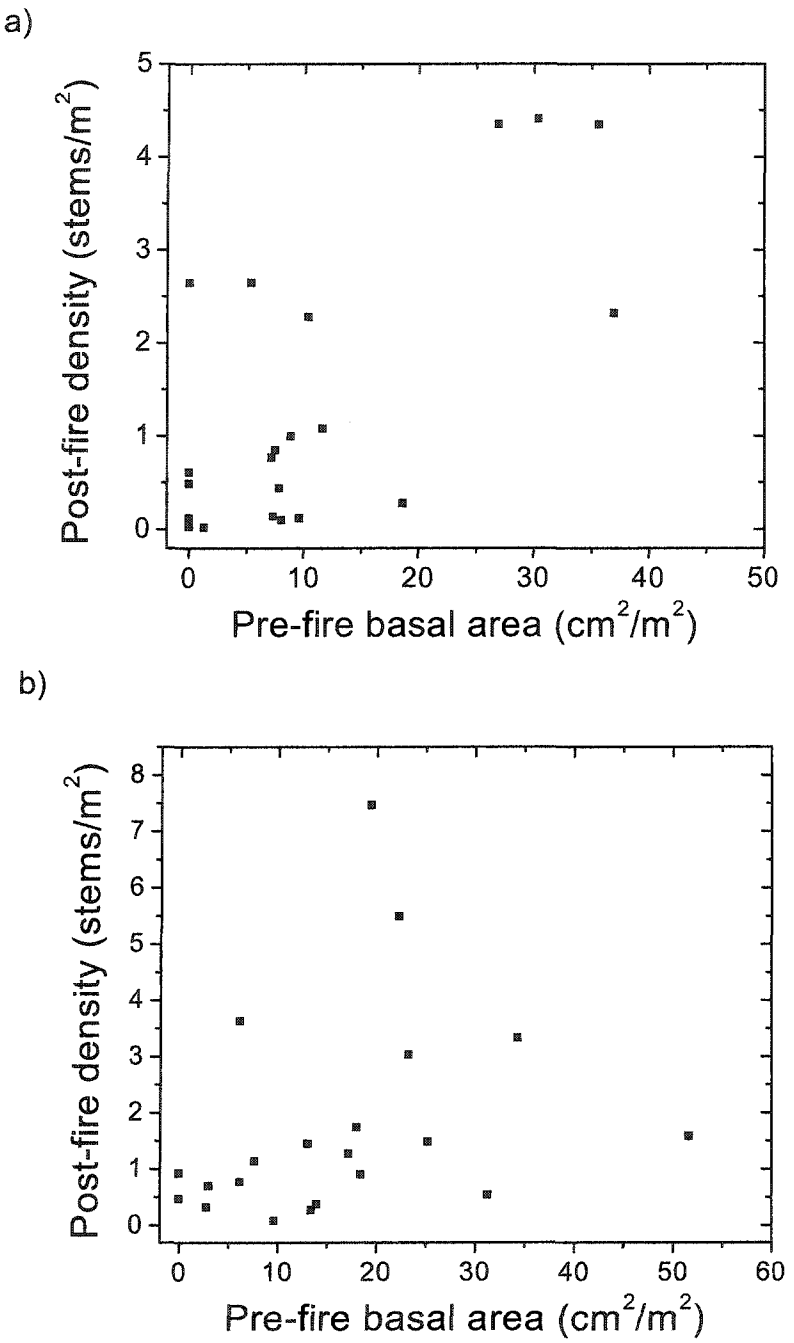

Figure 5.4: Post-fire stem density versus pre-fire basal area. Relationships are shown separately for (a) pine and (b) spruce. Post-fire densities are from 19 years after fire.

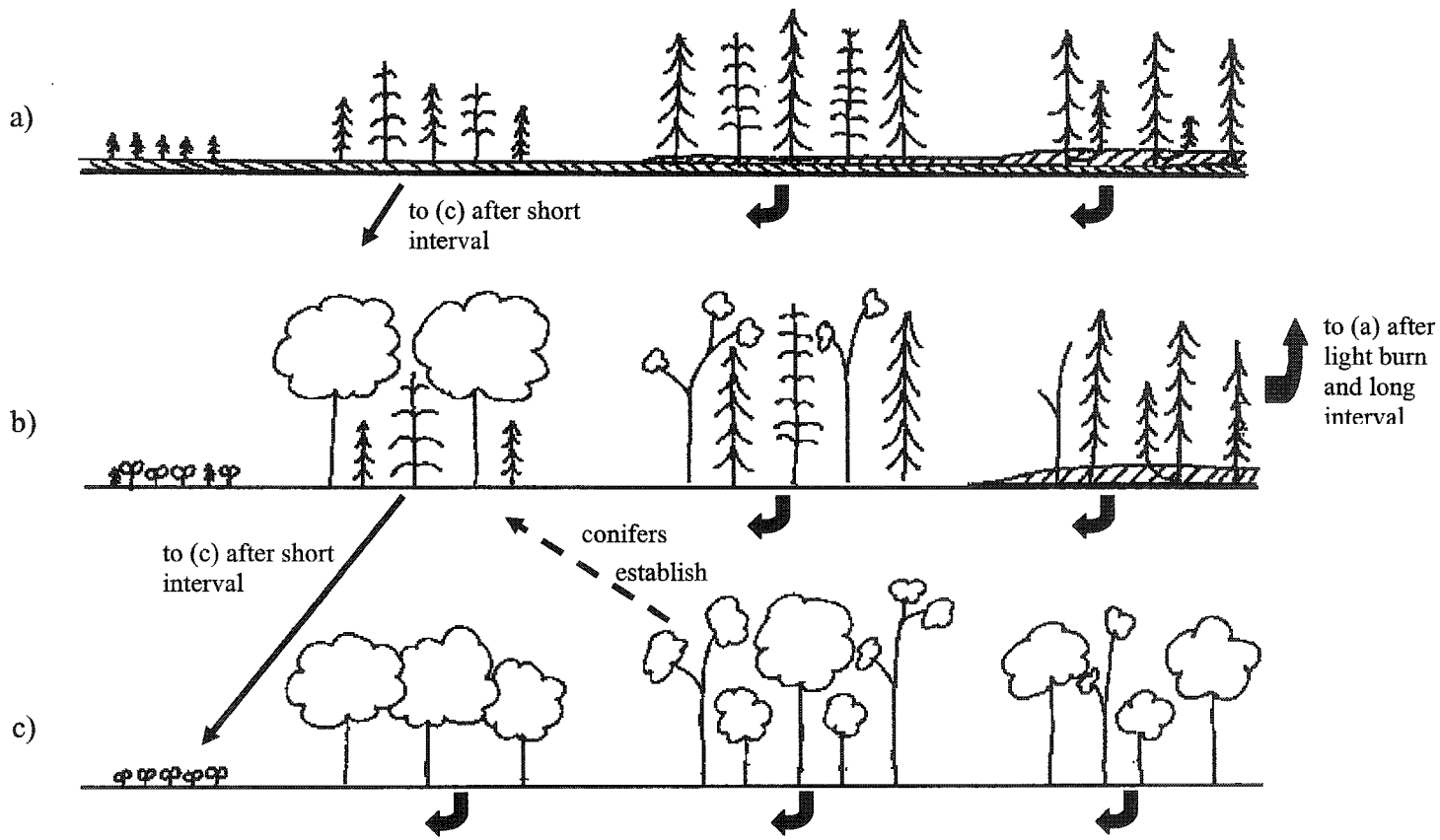

Figure 5.5: Schematic diagram showing successional pathways after fire. Succession pathways are divided into three generalized types: a) conifer-dominated, b) mixedwood (mixed conifer and deciduous), and c) deciduous-dominated. Progression from early to later stages is expected to occur along the path of a given trajectory, except where interrupted by fire (solid arrows) or, in the case of the deciduous trajectory, understory colonization by conifers (dashed arrow).

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CHAPTER 6: SUCCESSION DYNAMICS AT THE RANGE LIMIT OF LODGEPOLE PINE*

* Manuscript title: Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. Authors: J. F. Johnstone and F. S. Chapin, III. Submitted to Global Change Biology.

Abstract

Because species affect ecosystem functioning, understanding migration processes is a key component of predicting future ecosystem responses to climate change. This study provides evidence of range expansion under current climatic conditions of an indigenous species with strong ecosystem effects. Surveys of stands along the northern distribution limit of lodgepole pine (*Pinus contorta* var. *latifolia*) in central Yukon Territory, Canada showed consistent increases in pine dominance following fire. These patterns differed strongly from those observed at sites where pine has been present for several thousand years. Differences in species thinning rates are unlikely to account for the observed increases in pine dominance. Rates of pine regeneration at its range limits were equivalent to those of spruce, indicating a capacity for rapid local population expansion. The study also found no evidence of strong climatic limitation of pine population growth at the northern distributional limit. We interpret these data as evidence of current pine expansion at its range limits and conclude that the northern distribution of lodgepole pine is not in equilibrium with current climate. This study has implications for our ability to predict vegetation response to climate change when populations may lag in their response to climate.

Introduction

A major scientific challenge is to understand the causes, mechanisms, and ecosystem consequences of species migration in response to global environmental change. Modern and palaeoecological studies show that changes in species distributions can dramatically alter the structure and functioning of ecosystems, especially when a species has unique effects on environment or disturbance regime (Vitousek *et al.*, 1987; D'Antonio & Vitousek, 1992; Hu *et al.*, 2001). Plant species migrate individualistically, with rates that vary in time and space (Davis, 1981; Webb, 1987; Huntley, 1991). Such variations can reflect differences in climate forcing, climate response, and dispersal behavior. Improving our understanding of how dispersal dynamics (*e.g.* Clark *et al.*, 1998) and climate (*e.g.* Davis *et al.*, 1986) interact to drive migration rates is an important component of predicting future ecosystem response to global change.

Many vegetation models predict that plant species will migrate in response to future changes in climate (*e.g.* Kirilenko & Solomon, 1998; Shafer *et al.*, 2001; Malcolm *et al.*, 2002). These models frequently depict expected range distributions in equilibrium with climate, but are poor indicators of transient responses of species because they rarely consider non-climatic factors that affect distribution patterns and migration rates (Loehle & LeBlanc, 1996; Kirilenko & Solomon, 1998). The climate response functions that usually form the basis of these models are derived from current species distribution patterns (*e.g.* Woodward & Williams, 1987; Lenihan, 1993), a technique that implicitly

assumes that current species distributions are in equilibrium with climate and directly reflect climate limitation of growth or survival (Loehle & LeBlanc, 1996).

This study examines the population dynamics of a boreal tree species (lodgepole pine, *Pinus contorta* ssp. *latifolia*) at its northern distribution limits in order a) to assess whether its current distribution limits appear to be in equilibrium with climate or other limiting factors, and b) if a non-equilibrium is suggested, to gain insight into the population processes that occur along a transient distribution limit. The motivation for a study on lodgepole pine arises from earlier research on Holocene pollen records, which show that lodgepole pine appears to have arrived at sites in central Yukon Territory, Canada as recently as 300-400 yr BP (MacDonald & Cwynar, 1986, 1991). These dates represent the latest stage of an 1800 km northward migration that began near the southern border of Canada about 12,000 yr BP (MacDonald & Cwynar, 1986; MacDonald *et al.*, 1998). Lodgepole pine does not occur further north or west in interior Alaska, although the healthy growth and cone production of planted pines in this area (Alden, 1988) suggest that suitable habitat and climatic regime are present. These studies indicate that lodgepole pine may be continuing its Holocene expansion into modern time and that its northern distribution limits may not represent an equilibrium with current climate.

Continued migration of lodgepole pine has implications for understanding species migration response to long-term changes in climate and the roles played by migration lags in determining transient assemblages of vegetation communities. The presence of a non-equilibrium distribution edge would imply that empirical estimates of the climate envelope of this species (Lenihan, 1993; Thompson *et al.*, 1999; Sykes, 2001) may be

biased in their representation of the full potential range of the species. The migration dynamics of lodgepole pine are also important to consider with respect to changes in boreal ecosystem functioning. Boreal pines (lodgepole and jack pine, *Pinus banksiana*) have a unique set of traits that affect ecosystem processes in ways that are different than those of alternative forest dominants such as spruce (*Picea*) or deciduous trees (*Populus* and *Betula*). Changes in the distribution of pine would therefore be expected to have important feedbacks to ecosystem dynamics.

In this study, we test the hypothesis that lodgepole pine is currently migrating by comparing pine regeneration dynamics between sites located along the northern edge and those in the interior of its range in Yukon Territory, Canada. Estimates of local expansion rates and relationships between expansion and site conditions provide additional information on the population processes occurring along the range edge of this species.

Materials and Methods

Study area

The current distribution of interior lodgepole pine follows along the Rocky Mountain chain in North America from a southern limit in Colorado, USA to a northern limit in central Yukon Territory, Canada (Wheeler & Guries, 1982). Our sampling focuses on the northern populations of pine located in Yukon Territory and along the Yukon/British Columbia border (Figure 6.1). Regeneration of lodgepole pine is commonly associated with fire (Lotan & Perry, 1983), so we focused our sampling specifically on recently burned forest patches.

We used a multi-step procedure to select sample sites along the edge and in the interior of the northern lodgepole pine range. We first identified all road-accessible burns between 5 and 50 years of age in southern and central Yukon Territory using federal fire inventory maps (Indian and Northern Affairs Canada, Whitehorse, Yukon). We visually inspected burns to determine whether deadwood from the recent fire was sufficiently well-preserved to identify the genus of pre-fire individuals. We classed the resultant set of burns into one of three categories describing their position relative to the current pine distribution, as follows: 1) outside range: no evidence of pine being present, 2) range interior: burns that included or were adjacent to stands dominated (>50% cover) by mature lodgepole pine, and 3) range edge: sites with trace amounts of mature pine but with no dominant pine stands >0.5 ha (Figure 6.1). The resulting distribution of burns in these classes is generally consistent with published range maps of lodgepole pine (Wheeler & Guries, 1982; Cody, 1996). However it is important to note that pine is not evenly distributed within those range limits and the species is absent from many areas that appear to be suitable habitat (J. Johnstone, personal observations).

We sampled all road-accessible burns along the range edge that met our sample criteria, plus two additional, isolated burns that were accessed by boat along the Pelly River (Figure 6.1). The resultant sampel of range edge sites included 6 burns, ranging in age from 6 to 48 years. Within each burn, we sampled stands where pine was present in the pre-fire community, as evidenced by standing dead pine trees. In three of the burns, we sampled all accessible pine stands; in burns where pine was more widespread, we selected stands to represent the range of observed pine regeneration densities. We

measured a total of 17 stands, with 1 to 5 stands per burn. All of the selected stands experienced 100% mortality of standing trees as a result of the most recent fire. Ages of the pre-fire stands ranged from 60-130 years.

We sampled three burns located in the interior of the pine range along the Yukon/British Columbia border (Figure 6.1). These burns were the closest burns to the pine range edge that fit our sampling criteria. Pollen records indicate that pine has been present in the area for 2500-5000 years (MacDonald & Cwynar, 1986, 1991). Samples from the burns were obtained at sites where post-fire vegetation succession had been documented in an earlier study (Oswald & Brown, 1990). All three burns occurred in the same year, and were sampled 19 years after burning. In total, 24 stands were sampled that ranged in age from 70-130 years at the time of burning (Oswald & Brown, 1990; unpublished data).

Sample procedures

For sites along the pine range edge, we sampled five randomly-positioned 2x50 m transects (0.05 ha) within a 0.25 ha area in each stand and counted the total number of seedlings or saplings of each tree species. We pooled seedlings of black and white spruce (*Picea mariana* and *P. glauca*) because small seedlings of these two species could not be differentiated. In all but the oldest stands, aspen (*Populus tremuloides*) trees were the tallest individuals, followed by pine and then spruce. Species size distributions showed only occasional evidence of seedling establishment occurring later than 10 years after the burn, supporting our expectations of even-aged stands (Chapter 2). We recorded observations of dead post-fire seedlings as we encountered them. For dead seedlings, we

assessed whether mortality was caused by herbivory or some other factor by looking for evidence of browsed stem tips or compensatory branching.

We documented the composition and basal diameters of all trees in the pre-fire community from standing or fallen deadwood that had been rooted within a sampling transect prior to the fire. Genus determinations of dead trees were based on cone, bark and branching morphology. Dead trees of uncertain identity (6% of all sampled trees) were allocated to species categories according to the proportional composition of identified individuals. Black and white spruce were pooled because some black spruce individuals lack cones and cannot be readily differentiated from dead white spruce trees. We did not count trees that were dead at the time of the fire, judging from deep charring patterns on the bole. Together, pine, spruce and aspen accounted for 99% of tree composition in both pre- and post-fire stands.

We measured organic-layer depths at 55 points at 5 m intervals along the center line of each transect. The upper 15 cm of mineral soil was sampled using a 2.5 cm corer at five random points for laboratory analysis of soil pH and gravimetric moisture content at field capacity. The age of the pre-fire stand was determined from annual ring counts of 5-10 basal disks or tree cores (30 cm above the uppermost roots) obtained from a mixture of dead pine and spruce trees systematically sampled to represent the largest, and hence oldest, trees in the stand.

For sites in the range interior, we measured pre-fire basal diameters and post-fire stem density in a single 10x10 m plot within each stand. The plots were established one year after the sites were burned, and were haphazardly selected to represent a range of

pre-fire stand compositions and site conditions. Soil and site characteristics were measured at the time of plot establishment and are presented elsewhere (Oswald & Brown, 1990). All stands had lodgepole pine present in either the pre-fire or post-fire community, and were dominated by pine, spruce, or a mixture of the two. Spruce, pine and aspen represented 99% and 96% of stems in pre-fire and post-fire stands, respectively.

Data analysis

We tested for differences in the general pattern of succession between pine range edge and range interior sites by calculating the frequency of positive, neutral, or negative shifts in the proportion of pine relative to the total conifer count (pine+spruce) and of aspen relative to the total stem count (pine+spruce+aspen). Composition shifts were calculated as pairwise differences in the proportion of a given species in pre- and post-fire communities, respectively, within a stand. The use of pairwise, proportional differences allowed us to consistently compare succession changes across sites that spanned four orders of magnitude in species densities (Figure 6.2). Pairwise differences were classed into five categories of change, ranging from a decrease of >50% to an increase of >50%, and significant differences in frequencies were tested with a χ^2 test statistic (Conover, 1999). Summaries of mean pine:spruce ratios omitted stands with zero values for spruce because of its position in the denominator.

We evaluated possible relationships between post-fire regeneration density and pre-fire and site characteristics at the pine range edge using Spearman rank correlation coefficients, with a conservative significance threshold of α=0.01. We used a rank-based

correlation statistic because several variables had non-normal distributions that were not satisfactorily corrected with transformations. Site variations in slope and aspect were minimal and these characteristics were not included in the correlation analyses.

Results

Stands sampled along the edge of the pine range (Figure 6.1) were dominated by white or black spruce at the time of burning, with minor components of lodgepole pine and trembling aspen (Figure 6.2). Stem densities in both study areas show a general pattern of increased density following fire. This is a common pattern in forest succession, where initial recruitment occurs at high densities and stands subsequently thin through density-dependent mortality. There was substantial overlap in the ranges of species densities observed at sites along the pine range edge and in the range interior, although aspen was generally more common at the range edge sites.

Despite the similarity in absolute stem densities between the pine range edge and range interior, pairwise comparisons of species composition before and after fire indicate important differences in successional trajectory between the two regions. Sites in the pine range interior frequently showed no change in conifer composition after fire, and of those that did, there was an equal tendency of increasing or decreasing pine dominance (Figure 6.3). Sites along the pine range edge, however, showed a significantly different pattern (χ^2=20.7, $p<0.001$), in which 90% of the sampled stands experienced an increase in the proportion of pine after fire, and no stands showed a decrease in pine. This change represents a shift in the pine:spruce ratio at the pine range edge from a mean ± SE of 0.05

± 0.02 (n=17) in pre-fire stands to 4.79 ± 2.19 (n=16) in post-fire stands. In contrast, there was no significant shift in the mean pine:spruce ratio at sites in the range interior, with pre-fire communities averaging 2.72 ± 1.19 (n=20) and post-fire communities averaging 1.78 ± 0.54 (n=23).

It could be argued that the above comparisons are biased because stands with very little pre-fire pine at the range edge are being compared with stands covering a wide range of pre-fire pine densities in the range interior. To account for this, we performed the same comparisons using only those range interior sites that had pre-fire pine:spruce ratios falling within the range observed at the range edge sites (0 to 0.36). The resulting subset of 14 range interior sites shows a pattern of conifer composition change that is very similar to the full set of sites (Figure 6.2). Average pine:spruce ratios for this subset of interior sites significantly increased from pre-fire (mean ± SE of 0.07 ± 0.03, n=10) to post-fire (0.77 ± 0.09, n=13) communities, but this increase was significantly lower than that observed at the pine range edge (Wilcoxon paired-ranks test, Z=-3.45, p=0.006, n=10, 16).

The observed changes in aspen dominance following fire were more consistent between study areas than the changes in pine (Figure 6.3). The majority of sites in both regions showed an increase in the proportion of aspen following disturbance, and no sites exhibited a decrease in the proportion of aspen. However, more stands showed a positive increase in aspen dominance in the range edge area than in the range interior (χ^2=7.5, 0.05>p>0.01), probably related to the generally greater abundance of aspen at the range edge sites (Figure 6.2). Post-fire aspen densities (but not pine or spruce densities) were

negatively correlated with post-fire stand ages of sites along the pine range edge (Spearman r = -0.78, p=0.0002).

Pine regeneration density at sites along the pine distribution edge was not significantly correlated with any of the environmental or stand factors that we measured, with the exception of soil moisture content at field capacity. Both pine and spruce densities tended to be higher on soils with greater moisture-holding capacity (r = 0.77 and 0.67, p = 0.0003 and 0.0035, respectively).

Discussion

We observed large increases in aspen density after fire at the majority of our sample sites (Figure 6.2). A pulse of high aspen recruitment after disturbance is a common feature of normal succession development in boreal stands and reflects aspen's capacity for prolific root-sprouting (Zasada *et al.*, 1992; Greene & Johnson, 1999). The fact that all of our sites had low densities of pre-fire aspen is consistent with studies showing high rates of aspen mortality over time, particularly in mixed deciduous/conifer stands (Greene & Johnson, 1999; Yao *et al.*, 2001). The negative correlation we observed between aspen densities and post-fire stand age provides additional support that substantial thinning of aspen was occurring during early succession at our sites.

In contrast to aspen, we expect stable patterns of relative dominance among conifers to be established shortly after fire and to persist through stand maturity. Trees in the boreal forest commonly establish during a brief 3-7 year window after fire, which is then followed by several decades of low recruitment (Lavoie & Sirois, 1998; Greene & Johnson, 1999; Gutsell & Johnson, 2002). Any subsequent changes in canopy dominance

that occur through succession are largely the result of species differences in growth rate and mortality (Van Cleve & Viereck, 1981; Gutsell & Johnson, 2002). There is little evidence that later establishment of understory trees is likely to alter patterns of canopy dominance in frequently-burned forests (Johnson & Fryer, 1989; Gutsell & Johnson, 2002).

Both pine and spruce have the capacity to dominate mature sites in the Yukon Territory (Oswald & Brown, 1986). Pine frequently has higher initial growth rates than spruce, and is thus able to reach the canopy earlier and establish dominance (Eis *et al.*, 1982; Gutsell & Johnson, 2002). In northern British Columbia, heights of white spruce do not begin to exceed those of lodgepole pine until 100 years of age (Eis *et al.*, 1982). Although there are no published fire cycle estimates for our study area, mean fire return intervals for nearby areas in Alaska and Alberta are estimated to range between 40-130 years (Yarie, 1981; Larsen, 1997). The mean pre-fire age of the stands we sampled was approximately 80 years (range 50-130 years). Given the current fire cycle, successional trajectories are too short to allow spruce to competitively exclude pine from the canopy of mature stands.

At least two factors, self-thinning and herbivory, could reduce conifer composition following initial establishment, but are unlikely to lead to spruce dominance during the relatively short intervals between fires. First, pine seedlings self-thin more rapidly than does spruce, but thinning rates decline dramatically once canopy dominance is established (Yao *et al.*, 2001). Pine reaches the canopy earlier than spruce because of its faster growth rate (Eis *et al.*, 1982; Wang *et al.*, 1994). Thinning is therefore unlikely

to reverse strong hierarchies in conifer dominance within the current fire cycle or to explain the 40-fold increase in median pine abundance in postfire prefire stands at the pine distribution edge. Secondly, other sources of species-specific mortality, such as herbivory, could reduce initial pine densities. Herbivory was most pronounced at one 48 year-old site, where snowshoe hares caused 50% mortality in pine and <5% in spruce. Although this site represents an extreme level of herbivory (herbivory-induced mortality at other sites was always <5% for both pine and spruce), initial pine densities were high enough that pine was still the dominant conifer when we sampled. Future herbivory at this site is expected to be limited because the surviving pine saplings have reached heights above those accessible to hares. In summary, although thinning and herbivory may influence stand densities, the hierarchies of conifer dominance observed in post-fire recruitment are likely to be maintained through succession to mature stands.

Succession in the boreal forest is commonly characterized as following a pattern of stand self-replacement, and mature forest composition is expected to vary little across multiple disturbance cycles in the absence of extreme disturbance events (Van Cleve & Viereck, 1981; Payette, 1992; Frelich & Reich, 1999). Even when forest composition is locally stable, however, we would expect individual stands to show some variability in composition after disturbance. Such variability can easily arise due to stochastic variations in seed availability, substrate conditions, mortality agents, or other factors (*e.g.* Zasada *et al.*, 1992). The pattern of conifer compositional change we observed at sites in the pine range interior is highly consistent with this type of dynamic equilibrium. There was no indication of a directional shift in conifer composition associated with fire

disturbance at these sites, as similar numbers of sites showed positive vs. negative changes in pine relative abundance. This pattern held even when only sites with low initial pine abundance were examined. Instead, patterns of variation in species composition at these sites appear to be related to variations in environmental conditions (Oswald and Brown, 1990).

In contrast, sites along the pine range edge showed consistent, large increases in the relative proportion of pine following fire and consequently, a strong directional shift in conifer composition. The magnitude of observed increases in pine dominance at the range edge were, on average, 4-fold larger than those observed for range interior sites with low pre-fire pine abundance. These large increases in pine abundance at the range edge are dramatic enough that many of the stands we sampled appear to be switching from dominance by spruce to dominance by pine within a single disturbance cycle. Such a clear directional shift strongly indicates a non-equilibrium succession dynamic in these stands. We suggest that the most reasonable explanation for this pattern is local population expansion associated with species migration. Movement of species range limits is expected to involve repeated colonization events, followed by population increases where site conditions are suitable (*e.g.* Clark *et al.*, 1998). Our observations of large, directional shifts in composition are consistent with expectations of local population increases along an active migration zone. Pollen records suggest that pine range limits reached the central Yukon during the past millenium (MacDonald and Cwynar, 1986, 1991), and current population expasions may simply represent the latest stages of Holocene pine migration. An alternative explanation, that pine is responding to

recent trends of increased warming (Serreze *et al.*, 2000) or fire disturbance (Weber and Flannigan, 1997) is also plausible, provided that populations at the range edge are more strongly limited by these factors than those in the range interior.

The lack of unique relationships between pine regeneration and environmental conditions provides additional indirect support for current migration activity. If pine were limited to its current distribution by site factors or climate, we would expect its regeneration performance to be more sensitive to environmental variations than spruce, whose range limits extend well beyond our study area. Our analysis indicated, however, that both pine and spruce are sensitive to the same site factors (soil moisture capacity). This relationship presumably reflects a positive effect of moisture availability on young seedling survival (Zasada *et al.*, 1992).

A comparison of absolute tree regeneration densities (Figure 6.2) indicates that pine populations at the range edge have a recruitment capacity that is similar to that of spruce, despite low pre-fire densities of pine that might ordinarily be interpreted as an indication of marginal site conditions for pine growth. Variations in pine regeneration density among range-edge sites were not correlated with pre-fire pine basal area, an index of on-site seed source strength (Greene & Johnson, 1999). Most of the stands we sampled were hundreds to thousands of meters distant from any nearby pine stands, so local seed rain would have been the primary seed source for post-fire pine regeneration. If seed availability is not an important driver of pine regeneration success, then single dispersal events that allow one or a few pine individuals to establish in a stand can have rapid and strong effects on future population densities. The presence of isolated pre-fire populations

of pine capable of large increases in population size fits a model of migration in which recurrent establishment and growth of outlier populations provides the primary mechanism of expansion. If the relatively slow Holocene migration rates of interior lodgepole pine (MacDonald *et al.*, 1998) represent a lag behind potential environmental limits, our data suggest these lags are more likely to be associated with low rates of dispersal success, rather than intrinsically low rates of population increase. In particular, the strong dependence of pine regeneration on fire disturbance (Lotan & Perry, 1983), combined with a patchy distribution of fires and habitat in the mountainous Cordilleran landscape may limit the frequency with which successful long-distance establishment events occur for this species.

Pine expansion into spruce-dominated forests is likely to cause important changes in ecosystem processes such as fire regime, forest productivity, and carbon storage. In western Canada, pine forests burn more frequently (Larsen, 1997) and generate larger fires (Cumming, 2001) than spruce forests. The serotinous cones of lodgepole pine store and release seed in response to heat, allowing pine to rapidly re-establish following fire (Lotan & Perry, 1983). This generates self-replacing stands with frequent fires and low soil carbon storage throughout the range of lodgepole pine (Lotan & Perry, 1983). Pine has higher nitrogen use efficiency than spruce (Bothwell *et al.*, 2001) and produces higher volumes of wood when grown on poor-quality sites (Wang *et al.*, 1994). Jack pine stands in central Canada are characterized by lower levels of organic layer accumulation and carbon storage on the forest floor than spruce stands (Trumbore & Harden, 1997). Because of these strong ecosystem effects, continued migration of lodgepole pine could

have important feedbacks to ecosystem functioning in spruce-dominated boreal forests that would not be predicted from direct effects of climate on ecosystem processes.

Conclusions

This study is one of the first examples of which we are aware that documents current expansion at the range edge of an indigenous species in a relatively pristine natural environment. Observations of post-fire stand regeneration at the edge and interior of the lodgepole pine range in Yukon Territory provide strong evidence of non-equilibrium population expansion of pine at its northern distribution limits. In conjuction with pollen records that estimate the arrival dates of pine in central Yukon to within the past millenium (MacDonald & Cwynar, 1986, 1991), this research suggests that lodgepole pine is continuing a trajectory of northern range expansion initiated in the early Holocene. This study has implications for how we interpret models of vegetation response to climate change. It provides an example of a species whose current range limits do not appear to be in equilibrium with modern climate and thus violates the assumptions implicit in the development of the climate-response functions used in many biogeographical models. The rapid rates of population growth that we observed for pine at its range limits also suggest that limitations on local expansion rates are unlikely to account for the slow migration rate of interior lodgepole pine during the Holocene. Instead, we hypothesize that dispersal dynamics and regeneration niche are factors likely to constrain pine migration dynamics. Our ability to predict future ecosystem responses to climate change at time scales relevant to society depends on improving our

understanding of the mechanisms, such as disturbance-dependent migration, that may cause species migration rates to lag behind their potential climate limits. Because of the important effects of species on ecosystem processes, species differences in migration behavior may emerge as a key factor controlling transient ecosystem response to global change.

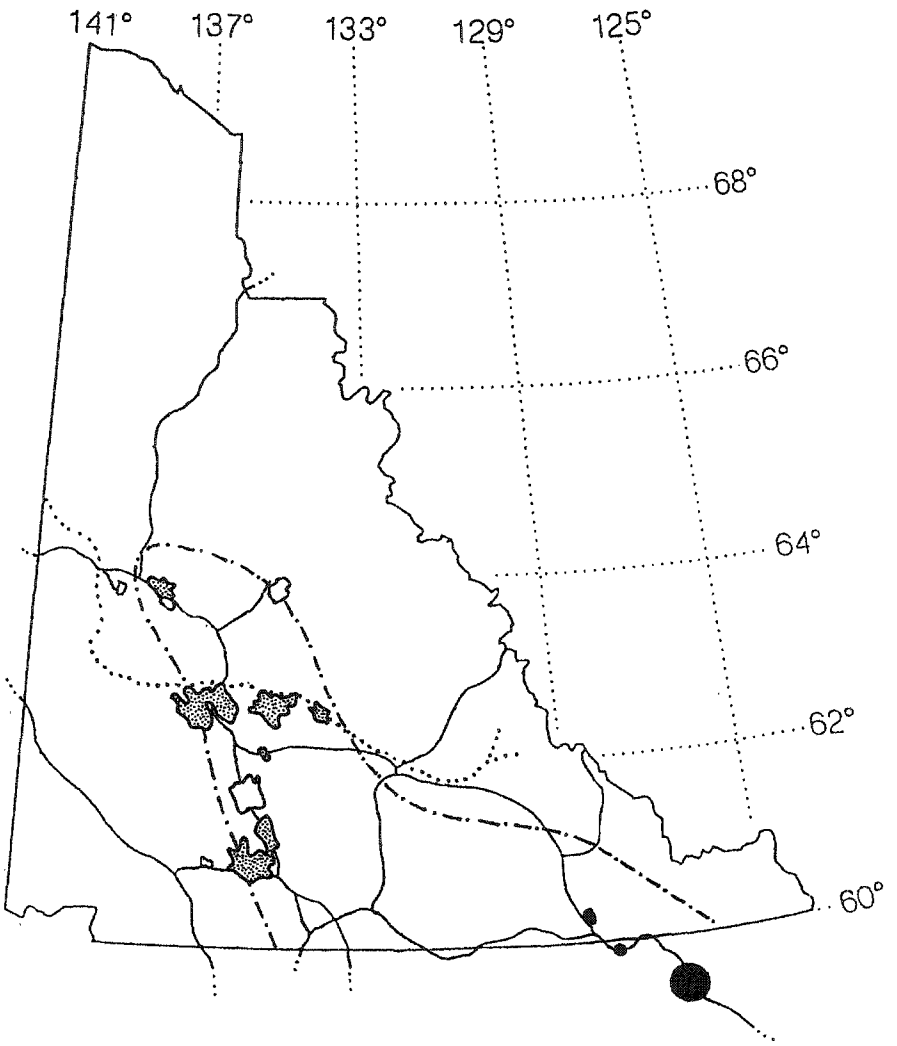

Figure 6.1: Map of Yukon Territory and study sites. Oblong shapes indicate the location of sample burns. The dash-and-dot line indicates the lodgepole pine distribution limits, solid lines show roads, and the dotted line indicates the Pelly River. The burns that are shown fit our criteria of accessibility, age restrictions, and preservation of deadwood. Unfilled shapes indicate burns where no pine was found (n=5), stipple-filled shapes indicate burns with scattered pine present (n=6), and solid-filled shapes are burns in areas of pine dominance (n=3). Burn locations are based on the Yukon Fire History database (Indian and Northern Affairs Canada, unpublished). Locations of burns in British Columbia are approximate. Lodgepole pine distribution limits are drawn to encompass published pine sample locations in Yukon Territory (Wheeler & Guries, 1982; MacDonald & Cwynar, 1986; Cody, 1996).

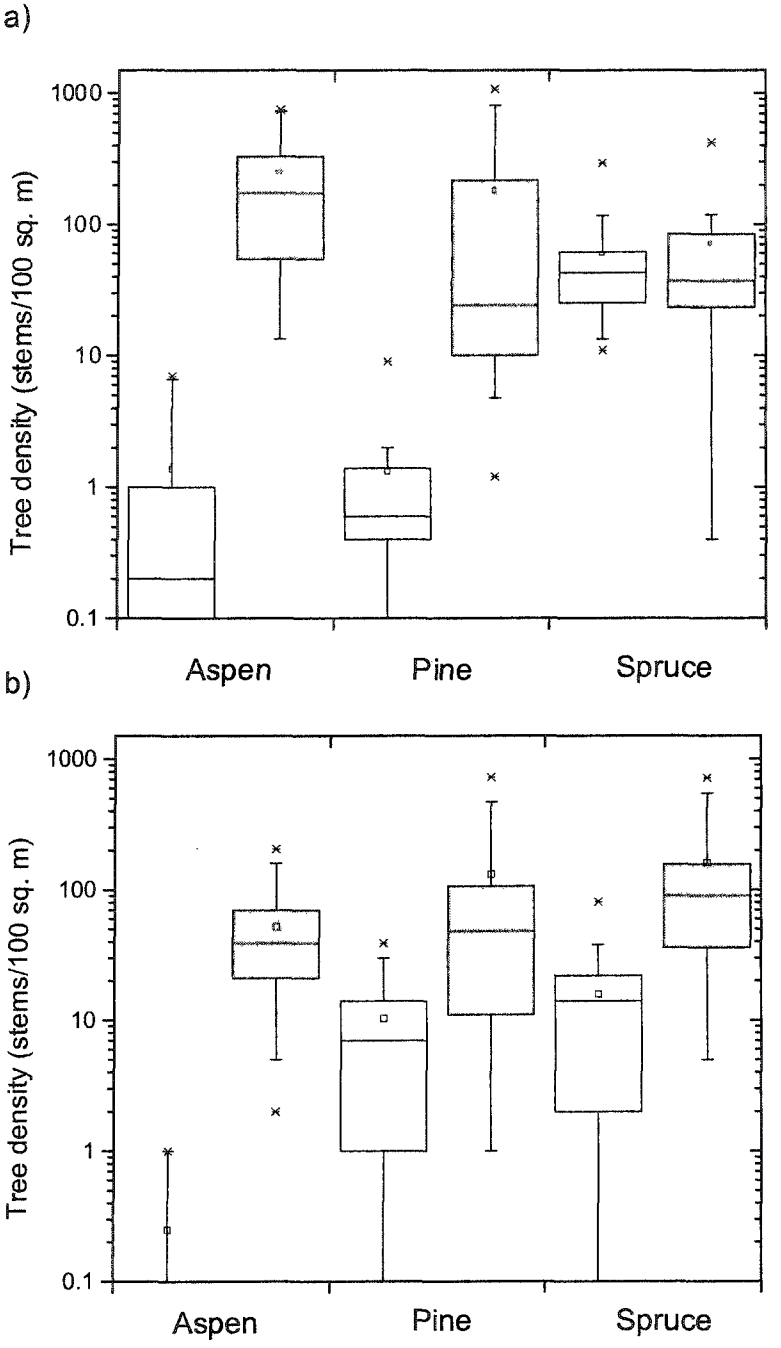

Figure 6.2: Box plot of pre-fire and post-fire density by species. Pre-fire(white boxes) and post-fire (shaded boxes) stem densities of aspen, spruce and pine are shown separately for stands located a) along the lodgepole pine range edge (n=17), and b) in the interior of the lodgepole pine range (n=23). The box area encompasses the 25% and 75% quartiles, the sample median is designated as a horizontal line inside the box, and sample mean is shown as an open square. Bars extending from the box encompass 95% of the observations, and additional ticks show extreme observations.

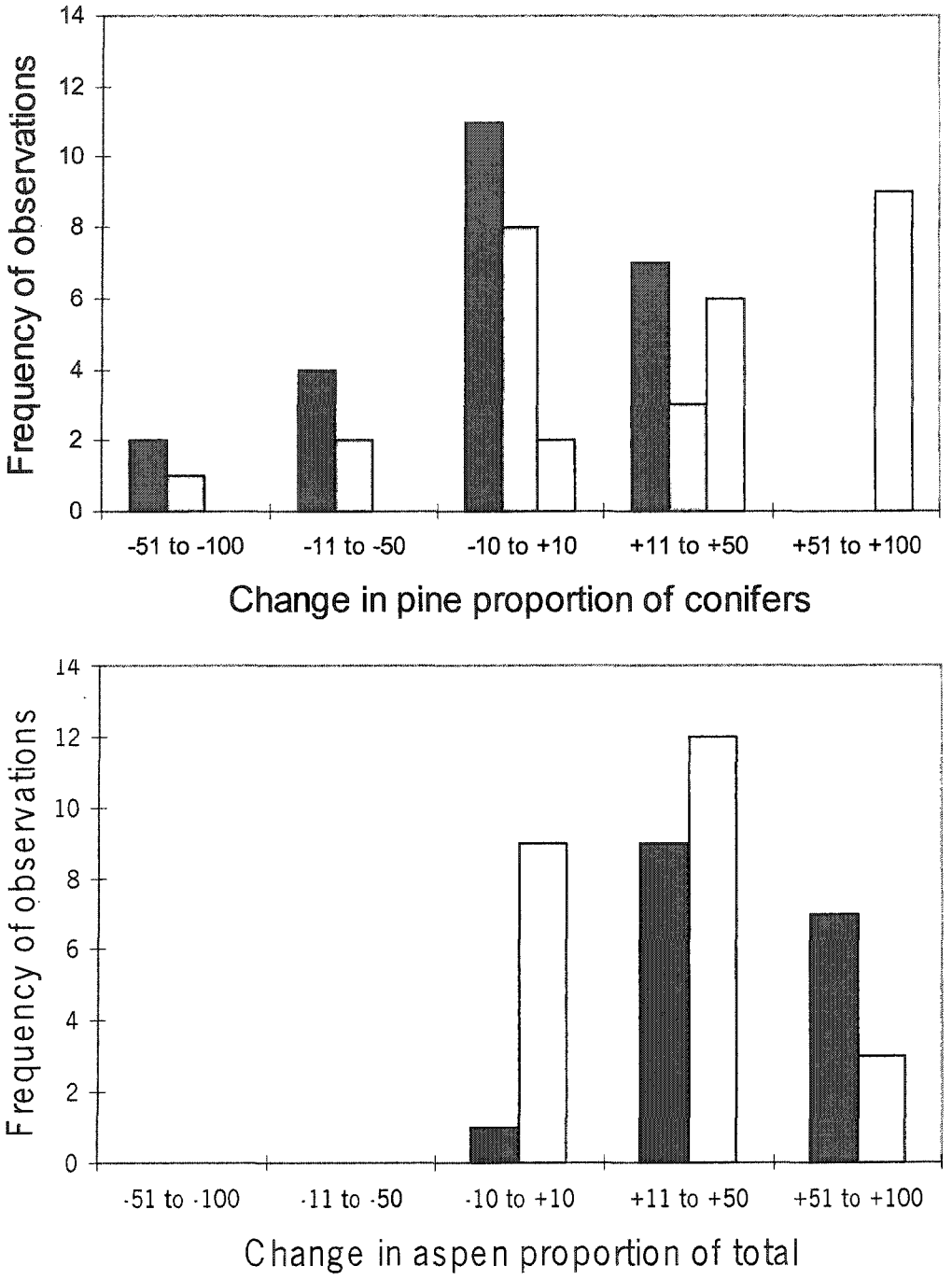

Figure 6.3: Histograms showing the frequency of different classes of change in post-fire stand composition relative to pre-fire composition. Changes in a) the proportion of pine relative to total conifers, and b) the proportion of aspen relative to total tree counts are shown separately for sites from the pine range edge (open bars) and range interior (black bars). Proportional changes in pine are also shown for a subset of range interior sites (grey bars; see results section)

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CHAPTER 7: CONCLUSIONS

Fire and climate change in boreal forest

The boreal forest is one of the most extensive biomes on earth (Whittaker, 1975). It plays an important role in global cycles, acting as a major reservoir of reactive soil carbon (McGuire *et al.*, 1995) and influencing large-scale climate and hydrological cycles by affecting patterns of surface heating and evapotranspiration (Bonan *et al.*, 1992; Chapin *et al.*, 2000). Northern regions are currently experiencing directional shifts in climate (Serreze *et al.*, 2000), and General Circulation Models predict that these areas will show the greatest magnitude of climate warming over the next century (Kattenberg *et al.*, 1996). Responses of boreal forests to climate change are of interest because of their potential influence on global or regional cycles of energy, water and carbon, and their local scale effects on forest resources and ecosystem services that are essential to the sustainability of human communities in the North.

Fire is the dominant natural disturbance agent initiating secondary succession in the boreal forest (Payette, 1992), and it has a widespread influence on the structure and composition of boreal landscapes (*e.g.* Niklasson and Granstrom, 2000; Weir *et al.*, 2000). Fire regime is directly affected by variations in climate at multiple scales, ranging from continental variations in fire cycle to weather effects on annual and daily fire activity (Van Wagner, 1983; Johnson, 1992; Johnson *et al.*, 1999). Paleoecological research indicates that past changes in climate have altered local fire regime (Johnson and Larsen, 1991; Larsen and MacDonald, 1998; Carcaillet *et al.*, 2001), and fire regime is predicted to respond similarly to human-induced changes in climate in the future (Flannigan *et al.*, 1998; Stocks *et al.*, 1998; Flannigan *et al.*, 2001). As a result, an

important component of boreal forest response to climate change is likely to be driven by fire effects on forest dynamics.

Succession trajectories in boreal forest: resilience vs. response

Variation in successional trajectories among boreal forest stands is believed to be tightly coupled to initial patterns of recruitment after disturbance (Dix and Swan, 1971; Viereck, 1973). In burned forests, post-fire tree establishment occurs as a short pulse of recruitment following fire, and recruitment in subsequent decades is frequently low or absent (Johnson and Fryer, 1989; Galipeau *et al.*, 1997; Lavoie and Sirois, 1998; Gutsell and Johnson, 2002; Chapter 2). Because the trees that establish first have a higher probability of reaching the forest canopy (Johnson *et al.*, 1994), patterns of early establishment have a strong impact on patterns of stand dominance later in succession (Johnson *et al.*, 1994; Gutsell and Johnson, 2002; Chapter 2). In most cases, post-fire establishment follows a pattern of stand self-replacement, due to environmental effects on species composition and regeneration feedbacks that favor the re-establishment of the pre-disturbance vegetation (Dix and Swan, 1971; Viereck, 1973; Greene and Johnson, 1999). Data from long-term observations presented in this thesis support these general patterns, showing evidence of self-replacement of species and communities under normal fire regimes (Chapter 5), and strong relationships between early establishment and subsequent stand composition (Chapter 2). Thus, successional dynamics in boreal forest appear to be commonly characterized by stable cycles of composition, or high resilience to fire disturbance, due to the frequent occurrence of strong, positive feedbacks between pre-disturbance and post-disturbance species composition (Frelich and Reich, 1999).

Fire plays a dual role in forest succession, both as an initiator of succession and as a factor that may directly influence patterns of vegetation regeneration. Under a stable fire regime, landscape patterns of species dominance are influenced by species adaptations for post-fire regeneration (Bergeron and Brisson, 1990; Bergeron, 1991; Suffling, 1995). This relationship is made more complex by the potential for vegetation to influence patterns of fire regime, either through species effects on landscape flammability (Mutch, 1970; Hély *et al.*, 2000; Wang, 2002), or through differences in growth rates that affect rates of fuel accumulation (Li *et al.*, 1997; Schimmel and Granström, 1997). The presence of feedbacks between vegetation and fire regime is likely to enhance the stability of boreal forest composition over time, by promoting fire regimes that favor the maintenance of the existing vegetation (*i.e.* Bergeron, 1991). However, it should be noted that few studies have been able to develop an independent test of vegetation effects on fire regime (Larsen, 1997), and the existence and importance of such effects have been critically challenged (Bessie and Johnson, 1995; Johnson *et al.*, 1998).

Under changing environmental conditions, fire disturbance may act as a force to disrupt the resilience of successional cycles in boreal forest and promote a directional response of vegetation to environmental change. Past responses of boreal ecosystems to climate change have been characterized by long lag periods, followed by sudden changes in vegetation that frequently coincide with fire events (Green, 1982; Camill and Clark, 2000; Payette *et al.*, 2001). This suggests that fire disturbance can act as a catalyst of vegetation response to environmental change, because of its ability to interrupt cycles of species maintenance and stimulate shifts to new vegetation regimes. For example,

unusual or extreme fire events may alter patterns of vegetation regeneration by influencing the supply of propagules available for regeneration (Viereck, 1983; Zasada *et al.*, 1992). Research in this thesis documents rapid shifts in post-fire successional trajectory following an abnormally short fire interval, providing evidence of the potential for extreme fire events to alter stable cycles of composition by disrupting regeneration cycles (Chapter 5). Mechanisms that might reinforce fire-initiated shifts from conifer- to deciduous-dominated trajectories were explored through an experimental test of aspen competitive effects on conifer seedling establishment (Chapter 3). Evidence from these two studies suggests that increases in fire frequency have the potential to directly alter the proportion of deciduous and coniferous communities on the landscape, and alternative community types, once initiated, could be maintained over time by a new set of regeneration feedbacks and competitive interactions.

The characteristics of individual fires may also directly influence patterns of vegetation change. Variations in fire severity can affect regeneration patterns by changing environmental conditions to favor alternative regeneration strategies (Viereck, 1983; Chapter 4) or by directly affecting the viability of propagules stored in the tree canopy (Arseneault, 2001) or forest floor (Schimmel and Granström, 1996). Experiments in this thesis examined the effects of fire severity on post-fire substrate conditions and consequent effects on seedling establishment. Results from these experiments indicate that light burns in organic-rich terrain are likely to favor the dominance of serotinous conifers, while severe burns permit the establishment of deciduous species and conifers dependent on off-site seed sources (Chapter 4). The study suggests that stable cycles of conifers may be favored by the accumulation and incomplete combustion of organic

layers across fire cycles. The results also point to the potential for rare, severe burns to initiate rapid changes in forest composition by providing openings for the establishment of off-site species. Thus, low levels of fire severity are likely to constrain ecosystem responses to climate change, while high severity burns may promote the development of new forest communities.

It is important to note that fire is not the only disturbance capable of altering successional trajectories in boreal forest. In particular, herbivory by mammals and insects may play an important role in driving compositional changes, and their effects may also be sensitive to changes in climate (Niemela *et al.*, 2001). Chapter 5 describes an example of an 'outlier' stand, in which the expected self-replacement of lodgepole pine was interrupted by hare herbivory during the first decade after fire. Twenty years after fire, there was no evidence of successful pine establishment, and herbivory at the site appeared to have switched its trajectory from conifer to deciduous dominance. Herbivores may also influence regeneration patterns by affecting the strength of plant competitive interactions. For example, competitive effects of aspen re-sprouts on conifer seedlings may be reduced by moose browsing on aspen, or increased by hare herbivory of slow-growing conifers in the deciduous understory (Chapter 3).

Zones of susceptibility and alternative stable states: Emerging landscape dynamics

An unresolved question in our understanding of boreal ecosystem dynamics is whether disturbance-triggered changes in successional trajectory are likely to represent transient effects on community structure or constitute new stable cycles that are maintained across disturbance intervals (*e.g.* Petraitis and Latham, 1999). Current theory suggests that forest communities with strong regeneration feedbacks are likely to have the

potential for more than one stable composition cycle (Frelich and Reich, 1999). This expectation is supported by research in this thesis, which provides evidence for the role of competition in maintaining deciduous-dominated trajectories (Chapter 3), and also points to local seed availability as an important factor maintaining conifer-dominated trajectories (Chapters 3 and 4). However, the likelihood that a switch in community composition represents a stable alternative state or a short-term perturbation will be dependent both on the scale of the disturbance (Petraitis and Latham, 1999) and the long-term importance of abiotic controls (Viereck, 1983). Thus, although the long-term dynamics of boreal forest ecosystems are likely to be shaped by interactions between disturbance and vegetation, these dynamics will also be constrained by the characteristics of the physical environment (Van Cleve *et al.*, 1991).

However, species also influence their environment (Chapin *et al.*, 1997), and the nature of environmental controls over species composition may be strongly influenced by the species themselves. For example, negative effects of deciduous litter on moss growth (Oechel and Van Cleve, 1986; Bonan and Korzuhin, 1989) may be an important factor that mediates between rapid or slow rates of organic matter accumulation in boreal stands, generating strong species effects on the soil environment (Bonan and Korzuhin, 1989; Van Cleve *et al.*, 1991; Mann and Plug, 1999). However, at sites where topography or soil characteristics exert strong controls over soil drainage, post-disturbance vegetation may always have a strong tendency to revert to moss-dominated, organic-rich communities after fire simply because the habitat is unable to support the long-term growth of alternative vegetation types (Viereck, 1983). Thus, the potential for fire to intiate stable, alternative vegetation communities is likely to vary across a landscape,

depending on abiotic conditions and overlapping species tolerances. Rapid vegetation responses and alternative stable states are most likely to occur at sites where abiotic conditions fall within the tolerance range of more than one potential type of dominant vegetation (Figure 7.1). These areas of potential niche overlap may constitute 'zones of susceptibility' on the landscape, where there is increased chance of compositional change. Empirical identification of such zones on a landscape is likely to be problematic, because species effects on the environment may create a false impression of strong environmental effects that may be weakened by a change in species composition.

The potential for vegetation response is also strongly affected by the available biota and therefore is likely to be influenced over time by patterns of species migration. Due to the time required for species range expansions, vegetation may lag in its potential response to environmental change until new species capable of dominance disperse to the region (Davis, 1984; Huntley, 1992). For example, the slow northern migration of lodgepole pine in response to Holocene warming, and current absence from interior Alaska, may obscure the potential for pine communities to become an important community type in Alaskan forests (Chapter 6; Alden, 1988). The strong performance of planted pine seedlings at several Alaskan sites (Chapters 3 & 4), and rapid population expansion of lodgepole pine along its current range edge (Chapter 6) indicate that pine migration has the potential to stimulate abrupt shifts in composition in spruce-dominated communities. Potential feedbacks between pine abundance and fire regime make the migration dynamics of this species an interesting case study of how interactions between climate, fire, and vegetation composition may influence long-term responses of boreal forests to climate change.

The research summarized in this thesis contributes to our understanding of boreal forest succession and the dynamic interactions that lead to post-fire resilience or post-fire response under changing environmental conditions. Studies of fire effects on succession trajectories have provided insights into the role of disturbance in maintaining or interrupting stable vegetation cycles and highlight some of the feedback mechanisms that form the basis of such cycles. Together, these studies promote a view of landscape dynamics in which the relative importance of abiotic controls and biological feedbacks may vary across a landscape and generate a mosaic of potential ecosystem responses to changes in climate. A more complete understanding of how disturbance, climate, and vegetation interact to control the dynamics of boreal forest landscapes is likely to greatly improve our ability to manage and predict ecosystem responses to climate change.

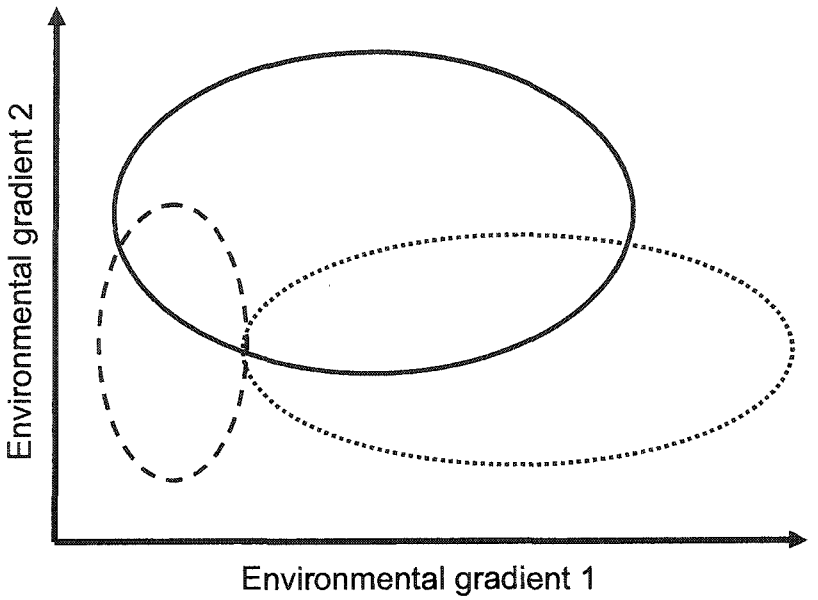

Figure 7.1: Theoretical species distributions across environmental gradients. Areas of overlap represent places where more than one species could dominate, generating 'zones of susceptibility' in which there is potential for switches in composition between alternative types.

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